

**SPATIAL AND TEMPORAL DIVERSITY TRENDS IN AN EXTRA-TROPICAL,
MEGATHERMAL VEGETATION TYPE: THE EARLY PALAEOGENE POLLEN
AND SPORE RECORD FROM THE US GULF COAST**

by

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ABSTRACT

During the early Palaeogene warm interval megathermal climatic regimes expanded beyond their current tropical limits. The early Palaeogene sporomorph (pollen and spore) record of the US Gulf Coastal Plain (GCP) indicates an extra-tropical vegetation type that developed under these megathermal climatic conditions. It is therefore suitable to address hypotheses concerning the importance of tropical climates in controlling low latitude spatial and temporal diversity patterns. Here, I construct a new sporomorph dataset comprising 151 samples, 41831 counted specimens and 214 sporomorph morphotypes. Fifty-nine of these morphotypes were not found in the published literature and are newly described. I demonstrate that previous studies of the GCP sporomorph record that have relied on biostratigraphic datasets have underestimated the true species richness of this region. Compositional heterogeneity was important for maintaining regional species richness on the GCP. The rate and scale dependency of spatial turnover in Holocene tropical and extra-tropical sporomorphs records precluded associating the GCP vegetation more closely with any particular modern biome, however. Finally, I show that warming extra-tropical regions to megathermal levels did not stimulate increased speciation there, which does not support a direct control of temperature on speciation rate in the low latitudes.

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CONTENTS

Chapter 1: Introduction	Page 1
1.1 The early Palaeogene greenhouse world	1
1.2 The US Gulf Coast paratropics	4
1.3 Global and regional climatic trends	6
1.4 Aims of thesis	9
1.5 Structure of thesis	11
 Chapter 2: Geological setting	 15
2.1 Structural and stratigraphic architecture of the GCP sedimentary sequence	15
2.2 Lithostratigraphy	17
2.3 Dating the GCP sedimentary succession	20
 Chapter 3: Materials	 23
3.1 Sampling strategy	23
3.2 Sample processing	27
3.3 Data collection	28
3.4 Potential reworking of sporomorphs	30
 Chapter 4: Systematics	 33
Trilete isospores	33
Zonoporate pollen	37

Tricolpate pollen	Page 39
Zonocolpate pollen	50
Tricolporate pollen	51
Zonocolporate pollen	81
Triprojectate pollen	85

Chapter 5: The Red Hills Mine palynoflora: a diverse swamp assemblage from the Late Paleocene of Mississippi

5.1. Introduction	93
5.2 Geological setting	96
5.3 Materials and methods	97
5.3.1 Rarefaction	97
5.3.2 Evenness	97
5.3.3 Non-metric multidimensional scaling (NMDS)	98
5.4 Results	99
5.5 Discussion	105
5.5.1 Environmental interpretation	105
5.5.2 Comparisons with other Late Paleocene palynofloras	107
5.6 Conclusions	109

Chapter 6: Regional-scale spatial heterogeneity in the Late Paleocene paratropical forests of the U.S. Gulf Coast

6.1 Introduction	111
6.2 Sampling spatial patterns in the fossil sporomorph record	115

6.3 Materials	Page 117
6.4 Age model	119
6.5 The biogeographic structure of the Paleocene GCP palynoflora	123
6.5.1 Methods	123
Additive diversity partitioning	124
Sample ordination - NMDS	128
Cluster analysis	129
6.5.2 Results	130
Additive diversity partitioning	130
NMDS	132
Cluster analysis	134
6.5.3 Compositional heterogeneity in the Paleocene GCP palynoflora	135
6.6 Relating the Paleocene GCP to Holocene biomes	139
6.6.1 Methods	139
Holocene dataset details	139
Data analysis	143
6.6.2 Results	146
6.6.3 The Paleocene GCP versus Holocene tropical and extra-tropical biomes	148
6.7 Summary and conclusions	150
 Chapter 7: An early Palaeogene record of extra-tropical plant diversity patterns	 153

7.1 Introduction	Page 153
7.2 Materials and methods	157
7.2.1 Dataset description and overview	157
7.2.2 Data analysis	158
Individual- and sample-based rarefaction	158
Within-sample evenness	159
Species richness estimation	165
NMDS	166
Proportional first and last appearances	167
Origins of first appearances: speciation versus immigration	169
7.3 Results	175
7.3.1 Palynofloral diversity on the GCP and in Colombia	175
Within-sample richness (observed)	175
Within-sample richness (estimated)	177
Within sample evenness	177
Within-Age richness (observed)	177
Within-Age richness (estimated)	180
7.3.2 GCP compositional changes	183
NMDS	183
GCP turnover (first and last appearances)	183
7.3.3 Immigration versus speciation on the GCP	185
7.4 Discussion and conclusions	188

7.4.1 GCP versus Neotropical diversity during the early Palaeogene	Page 188
7.4.2 The influence of temperature on paratropical speciation, and implications for the form and maintenance of the LDG	189
Chapter 8: Conclusions	193
8.1 Restatement of thesis aims	193
8.2 Major findings of thesis	193
APPENDIX 1: ADDITIONAL SYSTEMATICS	197
APPENDIX 2: R CODE	373
REFERENCES	401
CD (enclosed on inside back cover)	
R code as .rtf files	
Appendix 3: Count data and sample information	
Appendix 4: Taxon index list with occurrence information	

LIST OF FIGURES

Figure 1.1. $\delta^{18}\text{O}$ and estimated ice-free temperatures for the Cenozoic	Page 2
Figure 1.2. Reconstructed positions of the continents during the Early Eocene	2
Figure 1.3. Global and US Gulf Coastal Plain climatic trends during the early Palaeogene	8
Figure 2.1 Stratigraphy for the US Gulf Coastal Plain	18
Figure 3.1. Map of U.S. Gulf Coast showing sampling localities, and stratigraphic coverage for each locality	24
Figure 3.2. Sedimentary logs for cores and outcrops sampled	26
Figure 3.3. Sampling intensity for formations in Mississippi and Alabama (Porters Creek to Zilpha formations) and Texas (Calvert Bluff Formation)	29
Figure 5.1. Typical exposures of lignite beds in the Red Hills Mine	95
Figure 5.2. Individual-based rarefaction curves for Red Hills Mine samples	100
Figure 5.3. Rank/abundance plots for Red Hills Mine samples	102
Figure 5.4. Sample-based rarefaction curves for lignite and non-lignite samples	102
Figure 5.5. NMDS biplot of Red Hills Mine samples and selected taxa	104
Figure 6.1. β diversity (among-sample heterogeneity) and spatial turnover in ecological systems	113
Figure 6.2. Sampling coverage and biostratigraphic correlation	118

Figure 6.3. Sampling scheme used in Chapter 6	Page 126
Figure 6.4. Additive partitioning of species richness	131
Figure 6.5. NMDS plots of Late Paleocene GCP samples	131
Figure 6.6. NMDS plots of Tuscahoma and Calvert Bluff formations separately	133
Figure 6.7. Two-way cluster dendrogram plot of GCP samples and taxa	Facing p. 134
Figure 6.8. Incidence plots for the 15 most common taxa within the Tuscahoma and Calvert Bluff formations	136
Figure 6.9. Locality maps for Holocene lakes.	142
Figure 6.10. Distance-decay plots for Holocene biomes	147
Figure 7.1. Box-and-whisker plots showing within-sample diversity (richness and evenness) information for the GCP and Colombia	176
Figure 7.2. Sample-based rarefaction curves, showing within-Age richness for the GCP and Colombia	178
Figure 7.3. Sample-based rarefaction curves for each site within each time bin	179
Figure 7.4. Chao2 estimated within-Age species richness curves for the GCP and Colombia	181
Figure 7.5. Chao2 estimated species richness curves for each site within each time bin	182
Figure 7.6. NMDS plot of samples from the GCP	184
Figure 7.7. Proportional first and last appearance data for GCP formations	184

Figure 7.8. Speciation versus immigration for GCP taxa

Page 186

Figure 7.9. Speciation versus immigration for GCP taxa, tabulated
by formation

187

Plates

Following p. 92

LIST OF TABLES

Table 5.1. Sample information for Red Hills Mine samples	Page 100
Table 6.1. Sample information for the Tuscaloosa and Calvert Bluff formations	120
Table 6.2. Sampling information for Holocene datasets	140
Table 6.3. Results for distance-decay regression of Holocene lake sites	148
Table 7.1. Sample information for GCP samples	160
Table 7.2. Taxon range and first appearance data for GCP taxa	170

CHAPTER 1: INTRODUCTION

1.1 The early Palaeogene greenhouse world

At the broadest scale, the climatic history of the Phanerozoic eon has been one of oscillations between 'icehouse' and 'greenhouse' climatic phases (Veizer et al., 2000). The latter, globally warm periods without major icecaps, account for the majority of the last 540 million years (Crowley, 2000). The most recent prolonged warm interval occurred from the Late Cretaceous to the early Palaeogene (Veizer et al., 2000); the Early Eocene Climatic Optimum (~50 – 52 Ma) is characterised by the highest global temperatures of the last 65 million years (Zachos et al., 2001; Zachos et al., 2008) (Fig. 1.1).

This warm phase, and in particular the more recent, Palaeogene part of it, has attracted considerable interest from palaeobiologists as a 'natural laboratory' in which to study the influence of climatic change on evolution, ecology and biogeography (e.g. Wilf, 2000; Crouch et al., 2001; Harrington, 2001; Bowen et al., 2002; Harrington, 2004; Greenwood et al., 2005; Wing et al., 2005; Gibbs et al., 2006; Gingerich, 2006; Yans et al., 2006; Harrington and Jaramillo, 2007; Wilf, 2008; Sluijs and Brinkhuis, 2009; Webb et al., 2009; Peppe, 2010; Archibald et al., 2011). This is because (a) biotas from this interval have essentially modern compositions in terms of their major plant and animal groups (Wilf, 2000; Bowen et al., 2002; Jaramillo et al., 2010), (b) the arrangement of the continents was similar to that of today (Smith et al., 2004) (Fig 1.2), allowing biogeographic shifts to be understood in the context of, and applied to, the dispersal routes and barriers of the modern world (Smith et

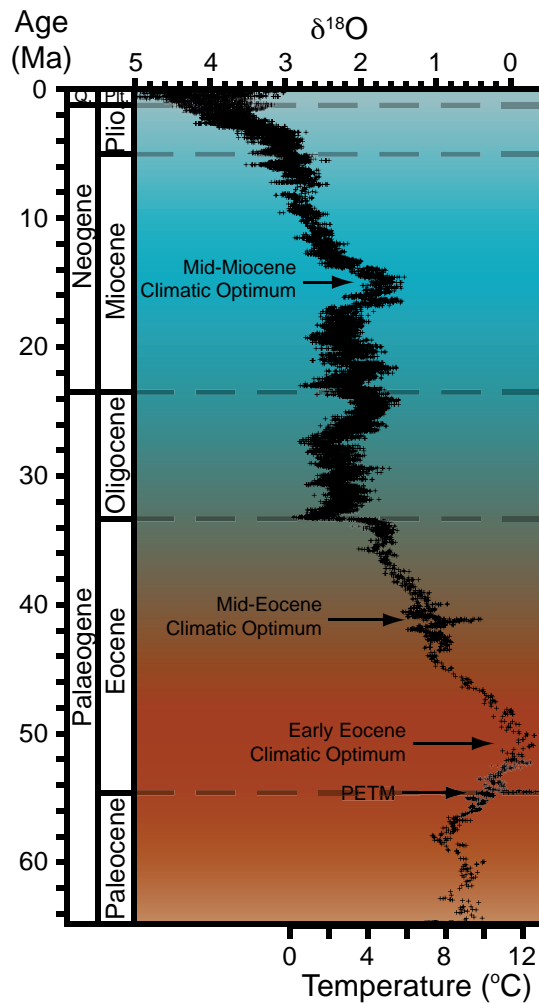


Figure 1.1. $\delta^{18}\text{O}$ and estimated ice-free temperatures for the Cenozoic, derived from benthic foraminifera. Redrawn from Zachos et al. (2008). Background colour provides an indication of global climatic state; red = greenhouse interval, blue = icehouse interval. Antarctic ice-sheet development is thought to have begun in the Middle to Late Eocene (Zachos et al., 2001; Zachos et al., 2008; Stickley et al., 2009). PETM = Paleocene-Eocene Thermal Maximum, Q = Quaternary, Plt = Pleistocene, Plio = Pliocene.

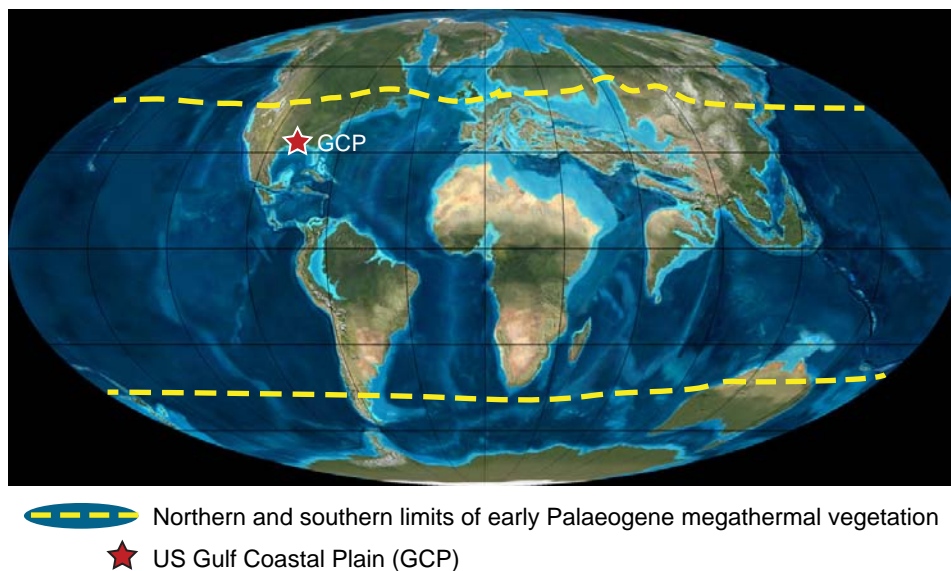


Figure 1.2. Reconstructed positions of the continents during the Early Eocene. Source: Ron Blakey (<http://jan.ucc.nau.edu/~rcb7/globaltext2.html>). Yellow dashed lines show the northern and southern limits of megathermal vegetation during the early Palaeogene (Fine and Ree, 2006; Fine et al., 2008). Red star shows the location of the US Gulf Coastal Plain (GCP).

al., 2006; Beard, 2008; Archibald et al., 2011), (c) examples of both rapid (Kennett and Stott, 1991; Lourens et al., 2005; Zachos et al., 2006; Röhl et al., 2007; Edgar et al., 2010; Sexton et al., 2011) and long-term (Wilf, 2000; Wing et al., 2000; Zachos et al., 2001; Zachos et al., 2008) climatic changes are present, and (d) an abundance of well-preserved, well-dated sediments and fossil material are available for scientific study (e.g. Wilf, 2000; Wing et al., 2000; Zachos et al., 2001; Wing et al., 2005; Brinkhuis et al., 2006; Jaramillo et al., 2006; Röhl et al., 2007).

During the greenhouse phase of the early Palaeogene (Fig. 1.1), equable, megathermal climates spread out beyond their current tropical limits (Wolfe, 1978; Greenwood and Wing, 1995; Wolfe and Dilcher, 2000; Fricke and Wing, 2004; Ivany et al., 2004; Iglesias et al., 2007; Wang et al., 2010). Warm-adapted organisms expanded their ranges to polar areas (Estes and Hutchinson, 1980; Case, 1988; Poole and Cantrill, 2006), and broad bands of paratropical (extra-tropical megathermal) vegetation covered the mid-latitudes (Fig. 1.2), so that megathermal forests occupied approximately three times their current area (Johnson and Ellis, 2002; Wilf et al., 2003; Fine and Ree, 2006; Fine et al., 2008). This large-scale shift in latitudinal climatic gradients and zones presents an ideal opportunity to study in detail the spatial and temporal macroecological changes associated with global climatic reorganisations. In particular, the importance of megathermal climates for shaping patterns of tropical diversification and spatial heterogeneity can be ascertained by taking as a case study an extra-tropical area that became megathermal during the early Palaeogene.

1.2 The US Gulf Coast paratropics – an extra-tropical megathermal vegetation type

The US Gulf Coastal Plain (hereafter GCP; Fig. 1.2) is an ideal setting to study the impact of warming upon biotic assemblages. Positioned at a latitude of ~30°N since the beginning of the Cenozoic (Smith et al., 2004), the GCP formed part of the expanded megathermal climatic zone during the early Palaeogene (Wolfe, 1978; Wolfe and Dilcher, 2000; Kobashi et al., 2001; Ivany et al., 2003; Ivany et al., 2004), and has an excellent fossil and sedimentary record that has been researched for over a century (e.g. Vaughn, 1900; Stephenson, 1915; Berry, 1916; Trowbridge, 1932; Cushman, 1951; Mancini, 1981; Mancini and Oliver, 1981; Gibson et al., 1982; Mancini, 1984; Mancini and Tew, 1990, 1991, 1995; Thompson, 1995; Dockery, 1998; Kobashi et al., 2001; Warwick et al., 2002; Kobashi et al., 2004).

The well-preserved sporomorph (pollen and spore) record of the GCP (Frederiksen, 1988; 1994b; Harrington, 2001; Harrington and Jaramillo, 2007) is of particular importance, because it provides the means of understanding the patterns and processes of terrestrial plant diversity and compositional change over extended periods of time. This is essential because plants form the base of food webs in most terrestrial settings, and thus have a critical role in ecosystem functioning (Wing and Tiffney, 1987; Wilf et al., 2001; Wilf and Johnson, 2004; Wilf, 2008), as well as being key components of the global carbon cycle (Beerling, 1998; Bonan, 2008; Prentice et al., 2011), and important mediators of climate feedback mechanisms through albedo and evapotranspiration effects (Crowley, 2000; Hoffmann and Jackson, 2000; Bonan, 2008; Bounoua et al., 2010). Sporomorphs are widely dispersed by many plant species and are deposited in a variety of sedimentary settings, and furthermore have an

excellent preservation potential (Traverse, 1988; Jarzen and Nichols, 1996). Although the sporomorph record has a lower taxonomic resolution than the plant megafossil record (Traverse, 1988; Lidgard and Crane, 1990; Gosling et al., 2009; Mander et al., 2010), the near ubiquitous presence of sporomorphs in fine-grained continental to near-shore marine sediments makes them an excellent tool for studying floral diversity and biogeography at a variety of spatial and temporal scales (e.g. Mayle et al., 2000; Colinvaux and De Oliveira, 2001; Wing and Harrington, 2001; Jaramillo, 2002; Harrington, 2003a, 2004; Jackson and Williams, 2004; Jaramillo et al., 2006; Gosling et al., 2009; Jaramillo et al., 2010; Mander et al., 2010).

Most previous studies of GCP palynology have focused on systematic descriptions of taxa (Engelhardt, 1964; Stover et al., 1966; Elsik, 1968a, b; Fairchild and Elsik, 1969; Srivastava, 1972; Nichols, 1973; Tschudy, 1973a, b; Elsik, 1974a; Elsik and Dilcher, 1974; Tschudy, 1975; Frederiksen, 1978; Frederiksen and Christopher, 1978; Christopher et al., 1980; Frederiksen, 1980a; Carroll, 1999), and/or biostratigraphic correlations across the GCP or with other regions (Frederiksen, 1979, 1980b, 1988, 1991, 1998; Elsik and Yancey, 2000; Elsik and Crabaugh, 2001), which has typically limited the taxonomic coverage to morphotypes that are common or have some biostratigraphic significance (or both). Where the emphasis has been on long-term biodiversity trends (Frederiksen, 1988; 1994b), raw counts were not made available, limiting the use of ecological techniques such as rarefaction (Gotelli and Colwell, 2001) and richness estimation (Colwell and Coddington, 1994) with these data. More recent analytical work on the GCP palynoflora has centred on short-term community change over the Paleocene-Eocene boundary, in relation to rapid

warming during the PETM (Paleocene-Eocene Thermal Maximum) (Harrington, 2001; Harrington and Kemp, 2001; Harrington, 2003b; Harrington et al., 2004; Harrington and Jaramillo, 2007; Harrington, 2008).

Thus to understand the influence of long-term global warming on extra-tropical floral diversity, there is a need to construct a new, taxonomically robust sporomorph dataset that extends over the early Palaeogene warming interval, that is amenable to the application of up-to-date analytical techniques. Here I mainly focus on the sedimentary record of the eastern GCP (specifically eastern Mississippi and western Alabama), because of its more complete and better-dated sporomorph record throughout the whole of the early Palaeogene. I have also sampled the Late Paleocene of the western GCP (Texas), in order to study spatial patterns of compositional heterogeneity across the GCP paratropics (see Chapter 6).

1.3 Global and regional climatic trends

Climate exerts a strong influence on plant assemblage composition and diversity, either directly through energy availability limiting primary productivity within an area (Currie et al., 1999; Allen et al., 2002), or by shaping individual taxon distributions at biogeographic scales (Prentice et al., 1991; Jackson and Williams, 2004; Punyasena et al., 2008). Therefore, to understand the influence of changing climates on regional plant diversity and composition, there is a requirement for accurate palaeoclimate proxies at both regional and global spatial scales.

At the global scale, mean annual temperature (MAT) trends for the early Palaeogene are well resolved through $\delta^{18}\text{O}$ records from benthic foraminifera (Zachos

et al., 2001; Zachos et al., 2008) (Figs. 1.1 and 1.3A). After a cool interval in the early Late Paleocene, global MAT increased to a plateau in the Early Eocene, and then gradually decreased into the Middle and Late Eocene. Superimposed on this broad-scale pattern are a number of rapid, transient, hyperthermals (Lourens et al., 2005; Sluijs et al., 2009; Sexton et al., 2011), the largest and best documented of which is the PETM (Kennett and Stott, 1991; Röhl et al., 2007). During this long-term global warming the latitudinal temperature gradient shallowed: the greatest temperature increases occurred at high latitudes (Fricke and Wing, 2004; Brinkhuis et al., 2006; Sluijs et al., 2006; Weijers et al., 2007; Sluijs et al., 2009), whereas the magnitude of low latitude warming is controversial but some increase in temperatures is known to have occurred (Ivany et al., 2004; Jaramillo et al., 2010).

Estimates for GCP climatic variables have been made based on leaf macrofossil morphologies (Wolfe, 1978; Wolfe and Dilcher, 2000) and $\delta^{18}\text{O}$ data derived from fish otoliths (Ivany et al., 2003), bivalves (Ivany et al., 2004) and gastropods (Kobashi et al., 2001). Wolfe and Dilcher (2000) used CLAMP analysis (Wolfe, 1990, 1995), a multivariate method that incorporates a range of morphological characters from fossil leaves, to estimate MAT, mean annual range of temperature (MART), and mean growing season precipitation (MGSP) for the early Palaeogene of Texas (summarised in Fig. 1.3B and C). Although useful, these estimates are limited by the lack of stratigraphic contextual information that was provided with the climatic data, and it is not clear what dating scheme Wolfe and Dilcher (2000) used. Three clear trends can be determined from these data, however. First, MAT on the GCP broadly followed that of the global curve, with a rise between the Middle Paleocene and Late

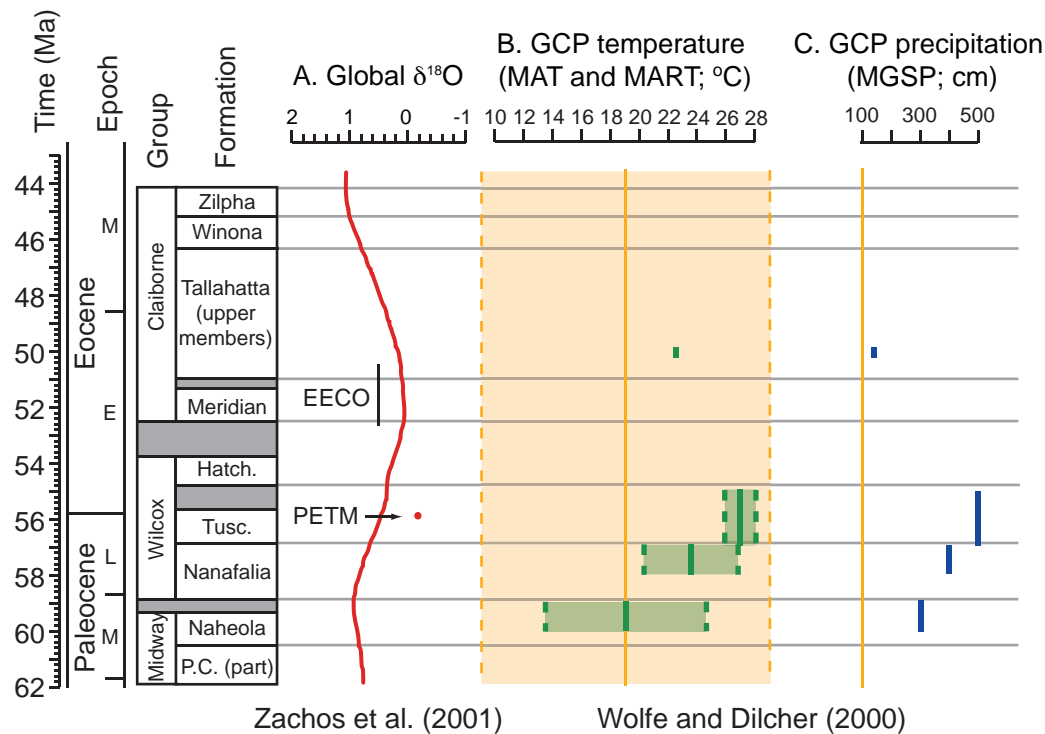


Figure 1.3. Global and US Gulf Coastal Plain (GCP) climatic trends during the early Palaeogene. The GCP stratigraphy is discussed in detail in Chapter 2. A, The global $\delta^{18}\text{O}$ curve is the running mean provided by Zachos et al. (2001), which gives an indication of MAT in an ice-free world (see also Figure 1.1). EECO = Early Eocene Climatic Optimum, PETM = Paleocene-Eocene Thermal Maximum. B and C, GCP temperature and precipitation are estimated from leaf morphologies and are taken from Wolfe and Dilcher (2000). B, Green solid line = estimated Palaeogene mean annual temperature (MAT), green dashed lines = estimated Palaeogene mean annual range of temperature (MART), orange solid and dashed lines = present day GCP MAT and MART, respectively. C, Blue lines = mean growing season precipitation (MGSP), orange line = present day GCP MGSP.

Paleocene/Early Eocene, and a subsequent decline into the Middle Eocene. Second, MAT, MART and MGSP correlate, with MGSP increasing with MAT, and MART decreasing (i.e. temperature regimes became less seasonal/more equable as MAT increased). Third, by the Late Paleocene/Early Eocene, MAT, MART and MGSP were all typical of modern tropical latitudes (Wolfe and Dilcher, 2000).

Estimates of MAT and MART from $\delta^{18}\text{O}$ records broadly support those from leaf fossils. Data for the Paleocene are currently sparse compared to the Eocene and Early Oligocene (e.g. Kobashi et al., 2001; Ivany et al., 2003), and the estimates of Ivany et al. (2003) were compromised by the choice of seawater $\delta^{18}\text{O}$ value used to calculate fractionation factors for the Early Eocene (J. Sessa pers. comm. 01/09/2010). However, a detailed study by Ivany et al. (2004) from the Early Eocene of the eastern GCP gave a robust MAT of 26°C and a MART of 2-3°C, which is comparable to the Late Paleocene estimate of Wolfe and Dilcher (2000). Ivany et al. (2004) further demonstrated that such a temperature regime is only found in the present-day within 19° of the equator, and listed Brazil and French Guiana as modern climatic analogues for the Early Eocene GCP. Thus by the Early Eocene Climatic Optimum the GCP was more or less tropical in terms of average temperature and seasonality, and probably in terms of precipitation as well.

1.4 Aims of thesis

Using an entirely new sporomorph dataset, the aims of this thesis are:

1. To document fully the early Palaeogene GCP sporomorph assemblage, and to describe any new taxa that are found (Chapter 4 and Appendix 1).

Rationale: to estimate accurately diversity and compositional trends, both within the GCP and in relation to other regions, requires a detailed dataset with a robust underlying taxonomy.

2. To test how a fully comprehensive sampling approach (e.g. counting all taxa in a sampling unit) alters our understanding of past biodiversity compared to biostratigraphic data collection (Chapter 5).

Rationale: previous studies of long-term palynological trends through the Palaeogene of the GCP have either focused on, or have been based on, biostratigraphic datasets (see above), which suggests that species richness on the GCP has been hitherto underestimated. It is therefore important to quantify the level of undersampling, both to establish a level of confidence in past estimates of GCP taxonomic richness, and to justify a more complete sampling approach.

3. To test the influence of temperature regime on the spatial distribution of biodiversity in extra-tropical floras, in relation to modern tropical and extra-tropical biomes (Chapter 6).

Rationale: climatic parameters correlate with the rate of spatial turnover in modern vegetation (Qian and Ricklefs, 2007), which in turn is intimately linked to the maintenance of regional species richness (Condit et al., 2005; Qian et al., 2005). Testing the impact of increased temperatures and equability on regional spatial patterns will provide information on the level of control that large-scale climatic changes exert on spatial compositional trends.

4. To test the relationship between MAT and diversity, speciation, extirpation and dispersal (Chapter 7).

Rationale: Tropical biodiversity is the highest in the world, and an increase in speciation rate with temperature has been hypothesised as causing this pattern (Gillooly et al., 2005; Allen et al., 2006). Evaluating the relationship between temperature and speciation rate throughout the early Palaeogene warming trend tests this hypothesis, and allows its wider implications to be considered in the context of changing global climatic phases.

1.5 Structure of thesis

This thesis has been planned as a series of publishable papers that each addresses a different question relating to extra-tropical warming during the early Palaeogene. Chapter 5 has already been published (Jardine and Harrington, 2008), and Chapter 6 has been accepted for publication (Jardine et al., *In press*). Chapter 7 is intended for publication, also as a paper, subsequent to the submission of this thesis, and a monograph is planned that will incorporate the systematic information and plates from this thesis (Chapter 4 and Appendix 1), as well as an overview of the geological setting and sampling details (Chapters 2 and 3).

Where possible I have left the content of the chapters as they were/will be submitted for publication, so that each can function as a stand-alone contribution. However, to remove redundancy in the text I have gathered all geological and sampling information together (Chapters 2 and 3, respectively), as well as compiling all literature cited into one reference list at the end of the thesis. I have described the analytical methods in the chapters where they are used; where the same methods are

used in subsequent chapters (e.g. rarefaction and NMDS), the reader is referred back to the previous description.

A number of taxonomic changes have occurred in the original dataset used for Jardine and Harrington (2008), largely through splitting or lumping together morphotypes as more slides were counted. I have therefore recounted and reanalysed the data for Chapter 5 prior to compiling it into the thesis. The results are almost identical to those presented in the original publication, however.

The structure of the remainder of this thesis is as follows:

Chapter 2 – Geological setting. Overview of the structural and stratigraphic architecture of the GCP, and the sedimentological sequence of the study interval.

Chapter 3 – Materials. Details of the locations, stratigraphy and sedimentology of the sampled cores and outcrops; sample processing protocols; and sporomorph counting procedures.

Chapter 4 – Systematics and Plates. Descriptions of all new taxa, and photomicrographs of the entire dataset.

Chapter 5 – The Red Hills Mine palynoflora: a diverse swamp assemblage from the Late Paleocene of Mississippi. A preliminary investigation, which demonstrates and justifies the sampling rationale used in this thesis, and provides detail on the taxonomic composition of the Late Paleocene GCP flora.

Chapter 6 – Regional-scale spatial heterogeneity in the Late Paleocene paratropical forests of the U.S. Gulf Coast. An analysis of the internal spatial structure of the Late Paleocene GCP palynoflora. Levels of compositional heterogeneity are compared with those in modern tropical and extra-tropical biomes, using the Holocene pollen

record as a proxy for the modern vegetation types.

Chapter 7 – An early Palaeogene record of extra-tropical plant diversity patterns.

A test of the influence of temperature on speciation and richness changes, as a driver of the latitudinal diversity gradient. Diversity, turnover and compositional change throughout the early Palaeogene on the eastern GCP are compared with coeval data from the Neotropics of Colombia.

Chapter 8 – Conclusions. Main conclusions from this thesis.

Appendix 1 – Additional systematics. Systematics of taxa already in the literature.

Includes brief synonymy lists, occurrence details and suggested botanical affinities.

Appendix 2 – R code used for data analysis. Included both in the thesis and on the enclosed CD as .rtf files.

Appendix 3 – Sample details and counts. Included on the enclosed CD as a Microsoft Excel file.

Appendix 4 – Taxon index and occurrence information. Included on the enclosed CD as a Microsoft Excel file.

Reference list. A compendium of all literature cited within this thesis.

CHAPTER 2: GEOLOGICAL SETTING

2.1 Structural and stratigraphic architecture of the GCP sedimentary sequence

The Palaeogene GCP sedimentary succession is a seaward dipping wedge of deltaic and marginal marine sediments, formed by the infilling of depositional basins on the passive southern margin of North America (Mancini and Tew, 1990; Galloway et al., 1991; Mancini and Tew, 1995). In southern Mississippi and southwestern Alabama, withdrawal and movement of the Jurassic Louann Salt in the Mississippi Interior Salt Basin, the dominant structural feature in the area, enhanced subsidence and created further accommodation space (Mancini and Tew, 1995). Palaeogene sediments crop out across the entire GCP, from Texas in the west to Florida in the east, curving up around the Mississippi embayment along the Louisiana/Mississippi border (Fig. 2.1).

During the early Palaeogene, prograding, fluvial-dominated delta complexes controlled siliciclastic sedimentation on both the eastern and western sides of the GCP (Fisher and McGowen, 1967; Mancini and Tew, 1991, 1995). In Mississippi and western Alabama, the deltaic sediments were sourced from northwest, and have been related to Laramide orogenic pulses in the Rocky Mountains (Mancini and Tew, 1995). Further to the east, in eastern Alabama, Georgia and Florida, carbonate sedimentation in a stable platform environment predominated; the siliciclastic- and carbonate-dominated lithofacies now 'intertongue' across southwestern Alabama (Mancini and Tew, 1991).

Much of eastern and southern Texas was dominated by the Rockdale Delta

system during the late Paleocene to Early Eocene, which was at least partly fed by the Mount Pleasant Fluvial System to the northeast (Fisher and McGowen, 1967; Nichols and Traverse, 1971). Flanking the delta system to the southwest and east are sediments representative of strandline, bay, and lagoon systems.

The overall stratigraphic architecture of the GCP is dominated by cyclical marine regressions and transgressions (Mancini and Tew, 1990, 1995; Breyer, 1997; Schulte, 2003; Schulte and Speijer, 2009). During regressions the delta complexes prograded and interdistributary swamps and coastal marshes developed (preserved as lignite deposits across the GCP; see Chapters 5 and 6) (Mancini, 1981; Mancini and Tew, 1995; Middleton and Luppens, 1995; Thompson, 1995; Breyer, 1997), whereas during transgressions the land was inundated and marginal marine deposition dominated. The GCP sedimentary succession is therefore one of repeated packages of lignites, clays, silts and sands, the latter often being calcareous, glauconitic and containing shelly marine fossils (Mancini, 1981; Mancini and Tew, 1995; Schulte, 2003).

Sequence stratigraphic concepts have been extensively applied to the sediments in Mississippi, Alabama and Texas (Mancini and Tew, 1991, 1995; Breyer, 1997; Crabaugh and Elsik, 2000; Schulte, 2003; Schulte and Speijer, 2009), and have revealed a succession of third-order unconformity bounded depositional sequences (Fig. 2.1A), which resulted from cyclical relative sea level changes. A number of local-scale, fourth- or fifth-order parasequences are superimposed on this sequence (Mancini and Tew, 1995). Relative sea level appears to have been controlled as much by local tectonics causing subsidence or uplift and erosion as by global (eustatic)

sea level changes, which has complicated attempts to correlate the GCP sequence stratigraphic framework with global sea level curves (Mancini and Tew, 1995; Schulte, 2003).

2.2 Lithostratigraphy

The sampled sedimentary sequence on the eastern GCP (eastern Mississippi and western Alabama) extends from the Porters Creek Formation (Midway Group) to the Zilpha Formation (Claiborne Group) (Fig. 2.1A; Chapter 3). Mancini and Tew (1990, 1991, 1995) have described in detail the early Palaeogene sedimentological sequence of Mississippi and Alabama. The lower, unnamed member of the Porters Creek Formation is primarily comprised of dark grey, massive clay. Conformably overlying this is the Matthews Landing Marl Member of the Porters Creek Formation, which comprises several metres of calcareous and glauconitic fine sands. The Naheola Formation conformably overlies the Porters Creek Formation and is the uppermost unit of the Midway Group. It is split into two members. The lower Oak Hill Member comprises interbedded micaceous, laminated silts and sands, with lignite seams occurring towards the top of the unit. The upper Coal Bluff Member consists of glauconitic micaceous fine sands and laminated silts and clays.

The overlying Wilcox Group contains the Nanafalia, Tusahoma and Hatchetigbee formations. The Nanafalia Formation unconformably overlies the Naheola Formation. The lowermost unit is the Gravel Creek Sand Member, which comprises medium to coarse-grained cross-bedded sands, and has been interpreted as an incised valley fill (Mancini and Tew, 1991). The middle member, informally

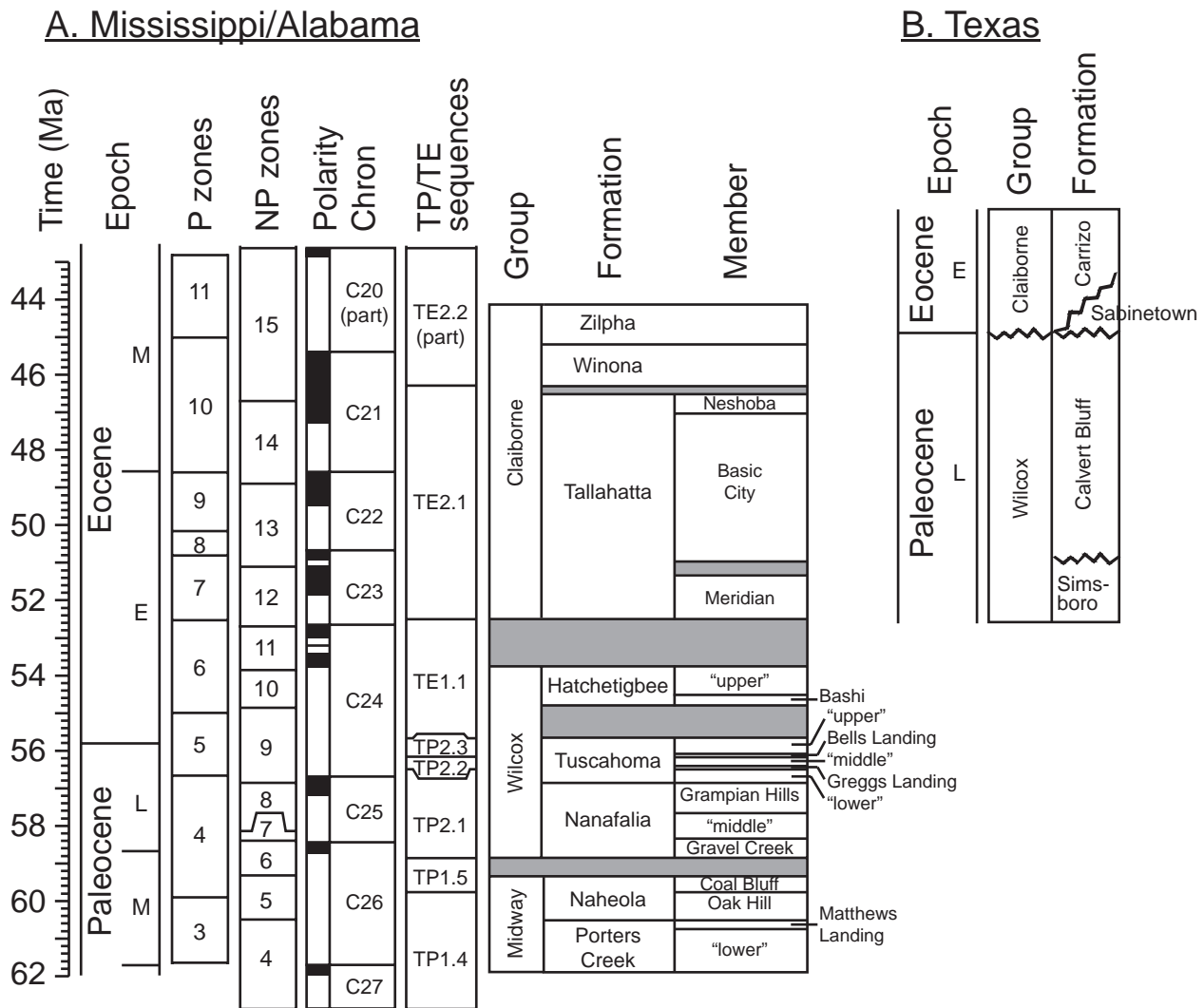


Figure 2.1 Stratigraphy for the US Gulf Coastal Plain. A, Mississippi and Alabama, showing from left to right: planktonic foraminiferal biozones (P zones) (Mancini and Oliver, 1981; Mancini, 1984; Berggren et al., 1985; Berggren et al., 1995), nannoplankton biozones (NP zones) (Gibson et al., 1982; Bybell and Gibson, 1985), magnetostratigraphic timescale (Rhodes et al., 1999) and sequence stratigraphy (Mancini and Tew, 1991), against the global timescale of Gradstein et al. (2004). Note that for sequence stratigraphy I have followed the TP/TE system of Mancini and Tew (1991) rather than the more recent TAGC (Tejas A; Gulf Coast) system of Mancini and Tew (1995), because the latter only extended to the Hatchetigbee Formation. TP2.1 = TAGC-2.1, TP2.2 = TAGC-2.2, TP2.3 = TAGC-2.3, TE1.1 = TAGC-2.4 (Mancini and Tew, 1995). B, Texas. Map at right shows the extent of the Paleocene and Eocene surface outcrop on the US Gulf Coast.

known as the “*Ostrea thirsae* beds”, comprises glauconitic, calcareous sands and silty clays, and the upper Grampian Hills Member consists of clays with thin beds of fine, glauconitic sand. The Tuscahoma Formation conformably overlies the Nanafalia Formation, and contains interlaminated clays, silts and glauconitic, calcareous fine-grained sands. Two of the sand units in the formation are named as the Greggs Landing Marl Member and the Bells Landing Marl Member. Thin beds of lignite occur in the upper part of the Tuscahoma Formation. The Hatchetigbee Formation unconformably overlies the Tuscahoma Formation, and is divided into the lower Bashi Member and an upper unnamed member. The Bashi Member comprises several metres of glauconitic, calcareous sands, and the upper member contains laminated micaceous clays, silts and fine-grained sands.

The sampled part of the Claiborne Group includes the Tallahatta, Winona and Zilpha formations. The Tallahatta Formation unconformably overlies the Hatchetigbee Formation, and is divided into three members. The lower Meridian Sand Member is comprised of clayey fine- to coarse-grained sands, the middle Basic City Shale Member consists of clays and silts, and the upper Neshoba Sand Member comprises micaceous fine-grained sands. The Winona Formation unconformably overlies the Tallahatta Formation, and consists of glauconitic medium to coarse sands. The overlying Zilpha Formation contains carbonaceous clays.

On the western GCP, sampling was limited to the Late Paleocene Calvert Bluff Formation (Wilcox Group) in east-central Texas (Fig. 2.1B). This formation comprises a suite of paralic sediments very similar to those found in the Tuscahoma Formation, with interbedded sands, silts, clays, as well as lignite horizons (Middleton

and Luppens, 1995; Warwick et al., 2002; Sturdy, 2006). The Calvert Bluff Formation is the main lignite-bearing unit in the Texas Gulf Coast (Middleton and Luppens, 1995); lignite seams occur in association with fluvial, deltaic and lagoonal sediments (Nichols and Traverse, 1971). The Calvert Bluff Formation formation is underlain by the Simsboro Formation and overlain by the Sabinetown Formation, although this latter unit is highly discontinuous in surface outcrop. Most upper contacts in the Calvert Bluff Formation are with the Carrizo Sand Formation (T. Stidham, pers. comm. 23/01/2009).

2.3 Dating the GCP sedimentary succession

The Paleogene sedimentary succession on the eastern GCP has been well dated through magnetostratigraphy (Rhodes et al., 1999), sequence stratigraphy (Mancini and Tew, 1991, 1995) and biostratigraphy using planktonic foraminifera (Mancini and Oliver, 1981; Mancini, 1984; Berggren et al., 1985; Berggren et al., 1995), calcareous nannoplankton (Gibson et al., 1982; Bybell and Gibson, 1985) and pollen (Frederiksen, 1980a; 1988, 1991, 1998; Harrington, 2001; 2003b; 2008) (summarised in Fig. 2.1A). Uncertainty still exists over the exact position of the Paleocene/Eocene boundary, although it is known to lie in the upper part of the Tusahoma Formation, as evidenced by the presence of early Wasatchian mammal teeth in the uppermost Tusahoma Formation at the Red Hot Truck Stop in Meridian, Mississippi (Beard, 2008). I have only sampled the upper Tusahoma Formation in the OSM#2 Wahalak core (see Chapter 3 and Figs. 3.1 and 3.2), in which the Paleocene/Eocene boundary is missing in the unconformity between the Tusahoma and Hatchetigbee formations

(Harrington et al. 2004). In this thesis I therefore treat the Paleocene/Eocene boundary as falling between these two formations, and all Tusahoma Formation samples as late Paleocene in age. There is also uncertainty over the precise lengths of unconformities on the eastern GCP; in Figure 2.1 I have put on the best estimates from the biostratigraphic literature (see also Frederiksen, 1988; p. 38-40).

The early Palaeogene succession on the western GCP is much more poorly dated, because calcareous microfossils are lacking from these sediments in Texas (Loeblich and Tappan 1957), and to date no magnetostratigraphic work has been published (Fig. 2.1B). It has therefore not been tied in to the global timescale with as much success as the eastern GCP. I address the age of the Calvert Bluff Formation in Chapter 6 (see section 6.4 Age Model).

CHAPTER 3: MATERIALS

3.1 Sampling strategy

The majority of sampling for this project took place on the GCP in May 2008. The locations of the sampling localities and their stratigraphic coverage are given in Figure 3.1; sedimentary logs are provided in Figure 3.2. Most sampling effort was focused on the better-dated sediments of the eastern Gulf Coast (Mississippi and Alabama), which form the basis for most of the analyses in this thesis. One hundred samples were gathered from five sediment cores that were cored from near the Mississippi/Alabama border: the OSM#1 Tuckabum core (Mancini, 1981, 1984) (Choctaw County, Alabama; 32°11'08"N, 88°10'22"W; 16 samples), the OSM#2 Wahalak core (Mancini, 1981, 1984; Carroll, 1999) (Choctaw County, Alabama; 32°03'00"N, 88°17'36"W; 61 samples), the Jasper deep core (Jasper County, Mississippi; precise location unknown; 8 samples), the Knight core (Lauderdale County, Mississippi; 32°20'09"N, 88°28'36"W; 8 samples), and the Harrell core (Lauderdale County, Mississippi; 32°15'42"N, 88°43'06"W; 8 samples).

I have also counted additional samples that were collected by Guy Harrington in November 2000. Fifteen are from the Hatchetigbee and Tallahatta formations in the Harrell core (Fig. 3.2), and eight samples are from field exposures of the Nanafalia and Tuscahoma formations in the Red Hills Mine (Ackerman, Mississippi; 33°22'42"N, 89°13'54"W). Sixty-two samples were collected in January 2007 from the Antioch Church core (Schulte, 2003; Schulte and Speijer, 2009), which was cored in Lowndes County, south-central Alabama, and covers the latest Maastrichtian Prairie

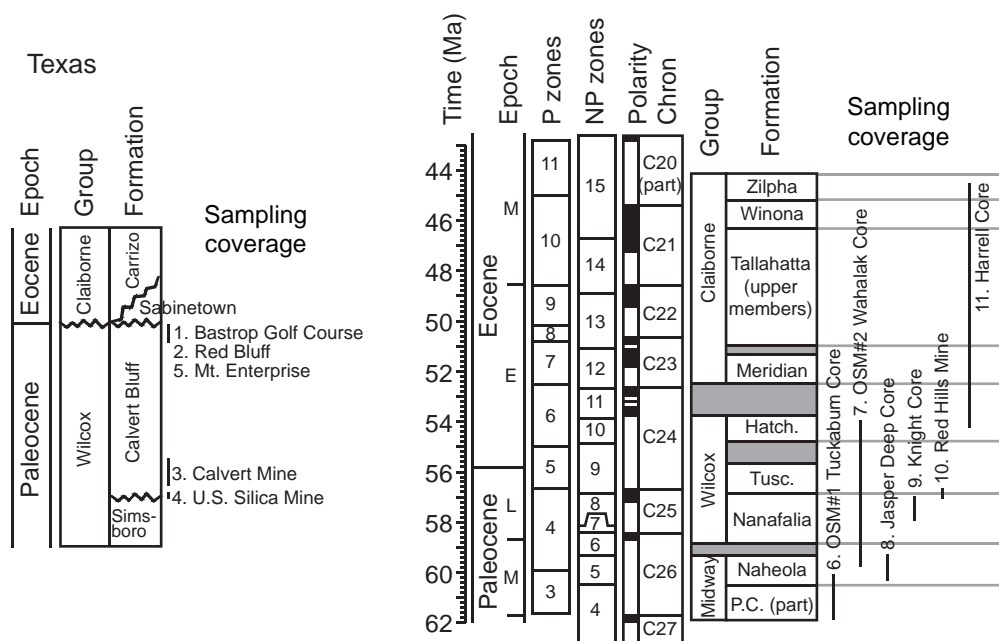
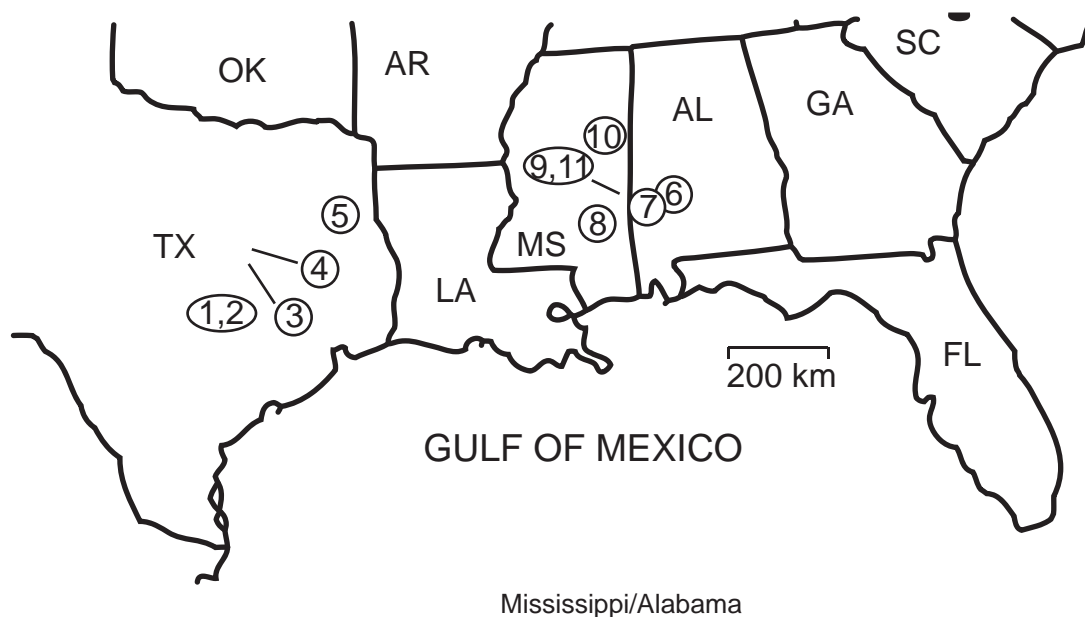


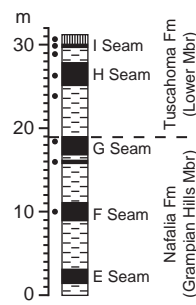
Figure 3.1. Map of U.S. Gulf Coast showing sampling localities, and stratigraphic coverage for each locality. Numbers on map correspond to locality numbers on stratigraphic sections; vertical lines represent sampling coverage. Details of the Gulf Coast stratigraphy are given in Chapter 2 (see also Fig. 2.1). P.C. = Porters Creek, Tusc. = Tusahoma, Hatch. = Hatchetigbee, Meridian = Meridian Sand Member of the Tallahatta Formation.

Bluff Formation to the base of the Naheola Formation (Schulte, 2003). All of these samples were barren for palynomorphs, however. Although sampling coverage was intended to be as stratigraphically complete as possible, no productive samples were gathered from the Neshoba Sand Member of the Tallahatta Formation or the Winona Formation (Fig. 3.2).

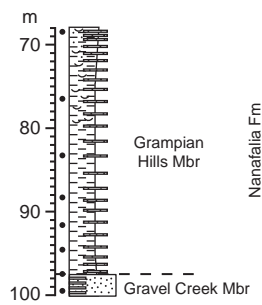
In contrast to the core-dominated sampling on the eastern Gulf Coast, all samples from the Calvert Bluff Formation of Texas were from field outcrops. Twenty-eight samples were gathered from five localities in east-central and east Texas: U.S. Silica Mine near Kosse (Limestone County; 31°18'30"N, 96°30'30"W; 1 sample), Walnut Creek Mining Company Calvert Mine near Bremond (Robertson County; 31°04'54"N, 96°39'30"W; 13 samples), Bastrop Golf Course in Bastrop (Bastrop County; 30°04'24"N, 97°16'54"W; 1 sample), Red Bluff on the Colorado River in Bastrop (Craddock, 1947) (Bastrop County; 30°04'18"N, 97°16'42"W; 10 samples), and a road cut eight miles north of Mt. Enterprise (Rusk County; 32°01'18"N, 94°43'24"W; 3 samples). The U.S. Silica Mine and Calvert Mine deposits are located near the base of the formation, and the Bastrop Golf Course, Red Bluff, and Mt. Enterprise sections are at the top of the formation, just below the contact with the Carrizo Formation (Craddock, 1947; Galloway, 2002). Although the Sabinetown Formation is typically placed between the Calvert Bluff and Carrizo Formations (Fairchild and Elsik, 1969; Elsik, 1978; Crabaugh and Elsik, 2000; Elsik and Crabaugh, 2001), it is highly discontinuous in surface outcrop and was absent from the sections sampled. Samples representing marine deposition in the upper part of the formation (Janus and Stidham, 2008) were barren of sporomorphs, limiting coverage to the formation

Mississippi

Red Hills Mine

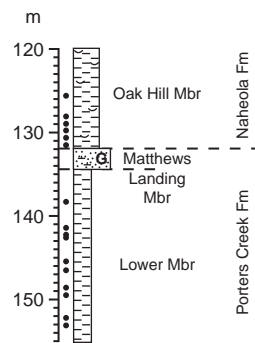


Knight Core

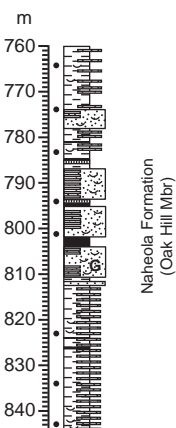


Alabama

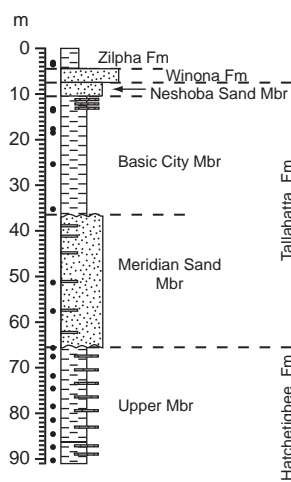
OSM#1 Tuckabum Core



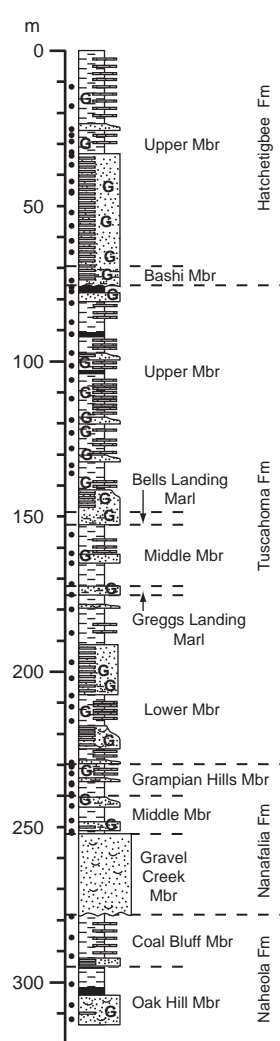
Jasper Deep Core



Harrell Core

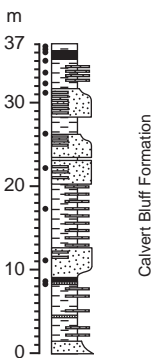


OSM#2 Wahalak Core

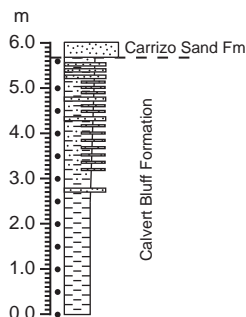


Texas

Calvert Mine



Bastrop Red Bluff



Key

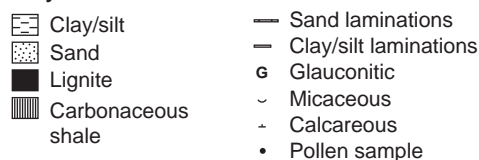


Figure 3.2. Sedimentary logs for cores and outcrops sampled, showing sampling positions. See sheet 'Sample_info' in Appendix 3 on accompanying CD for sample names. See also Chapter 2, section 2.2 for an overview of the lithostratigraphy of the GCP.

top and base.

Of the 123 samples from the eastern GCP, nine are lignites, all but one of which are from the Late Paleocene Nanafalia and Tuscahoma formations (see Chapter 5 for a detailed analysis of Late Paleocene GCP swamp floras preserved in lignite deposits). The remaining 114 samples are clastic sediments (clays, silts and fine sands, often interlaminated and with varying proportions of calcareous material; Fig. 3.2). Twenty-two of the Texas samples are clastic sediments (also interlaminated clays, silts, and sands) and six samples are lignites, with three lignite samples from the base of the formation (U.S. Silica Mine and Calvert Mine sections) and three from the top (Mt. Enterprise section).

3.2 Sample processing

Preparation of the clastic samples followed a basic procedure of maceration of 20 g of material with a mortar and pestle, successive treatments of 10% HCl, 40% HF, and 10% HCl to digest carbonates and silicates, and a light oxidation to remove excess amorphous organics (2 min in 70% HNO₃). Between most stages, residues were sieved with a 10 µm mesh. Lignite samples were processed by crushing finely 2 g of sediment, and oxidizing for 25 min in 70% HNO₃ and 10 s in household bleach. Residues were sieved at 10 µm after each oxidation treatment. Large fragments of carbonized material were sieved off with a 180-µm mesh. Finally residues were stained with safranin and aliquots were mounted onto coverslips.

3.3 Data collection

A target sample size of 300 sporomorph grains was set for each sample, although this was not reached for all slides (Fig. 3.3A). Pollen yields were lower for the lowermost and uppermost formations in the sequence (Fig. 3.3A), as is sampling intensity (Fig. 3.3B) and the number of localities per formation sampled (Fig. 3.1). Where one morphotype accounted for >100 grains, and where sample sizes permitted, counts were increased so that at least 200 grains of the non-dominant type were included. Slides were scanned after the main count to detect any taxa that were not encountered during the count, which provides a fuller picture of the assemblage composition.

In this thesis I am concerned primarily with identifying the possible taxonomic diversity and have avoided combining taxa (lumping) where possible and justified. However, where there is considerable overlap between form-species or form-genera I have grouped morphotypes into generalised taxonomic groups. For example, all morphospecies of *Triporopollenites* and *Triatriopollenites* were combined into a single Betulaceae/Myricaceae group, and all bisaccate grains of the general Pinaceae-type were grouped together. Details of all morphotypes used in this thesis, including justifications for informal groupings used, are in Chapter 4 and Appendix 1. All taxa are illustrated in Plates 1 to 14. Sporomorph photographs were taken on a Zeiss Axioskop 40 microscope at x1000 magnification and under phase contrast, unless otherwise stated in the Plate explanations. All taxa are indexed in Appendix 4 on the enclosed CD. For each taxon this index includes plate and figure information, the relevant page numbers for systematic details in Chapter 4 or Appendix 1, occurrence

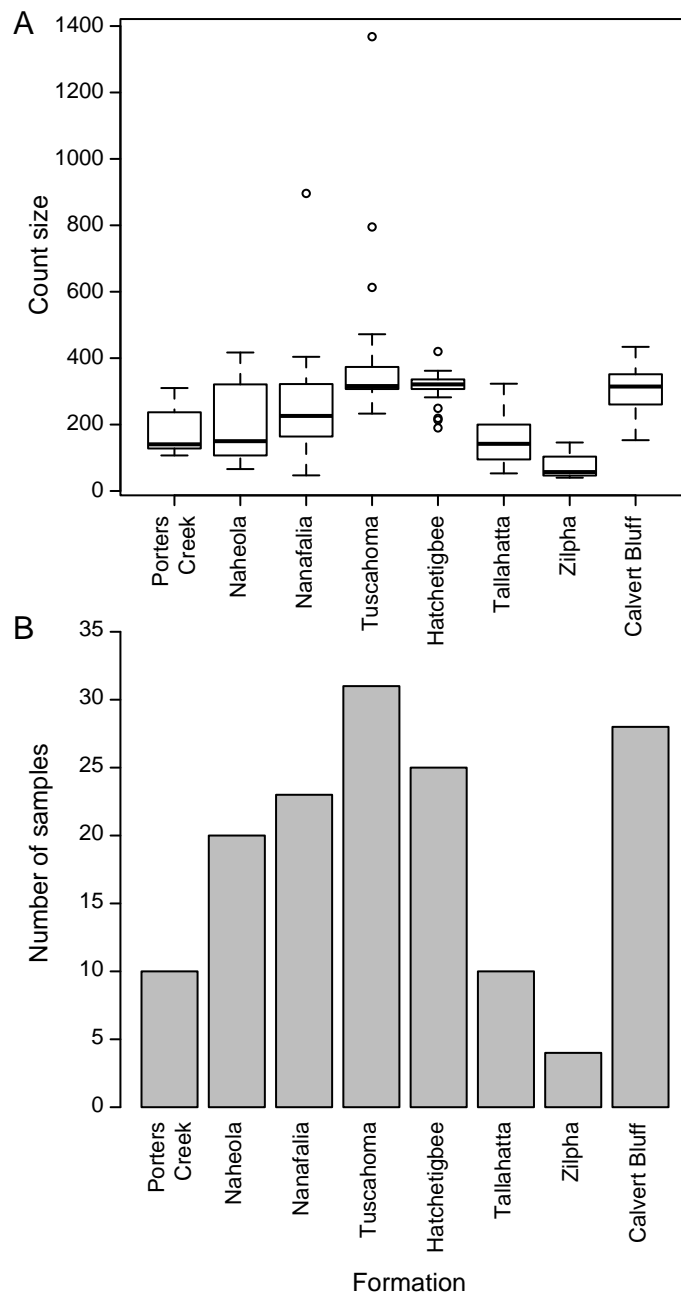


Figure 3.3. Sampling intensity for formations in Mississippi and Alabama (Porters Creek to Zilpha formations) and Texas (Calvert Bluff Formation). A, box and whisker plot of count sizes for each formation. For each formation the thick horizontal line shows the median value, the bottom and top of the box show the 25th and 75th percentiles, respectively, and the vertical dashed lines (the whiskers) show either the most extreme values or 1.5 times the interquartile range, whichever is smaller. Points more than 1.5 times the interquartile range below and above the 25th and 75th percentiles, respectively, are plotted individually as circles. B, bar chart of the number of samples within each formation.

data by formation, and the number of specimens counted.

The dataset comprises 41831 counted specimens from 151 samples. In total 213 sporomorph morphotypes were detected; 209 of these formed part of the main counts, and the remaining four were only recorded in post-count scans of the slides, and were not included in the analyses. They are described and illustrated along with all other taxa in the Systematics and Plates, however. Fifty-two of the 213 sporomorph taxa are singletons (represented by one specimen only).

All data analyses are described in the Methods sections of Chapters 5 to 7, along with the subsets of the dataset being used and any data vetting procedures. Numerical analysis was carried out using R, version 2.11.1 (R Development Core Team, 2010) with the package “vegan,” version 1.17-4 (Oksanen et al., 2010), unless otherwise stated. The R code used in these analyses is provided in Appendix 2, and the raw data are provided as a Microsoft Excel file on the enclosed CD (Appendix 3).

3.4 Potential reworking of sporomorphs

Sporomorphs are very susceptible to reworking (Traverse, 1988). Of the taxa in the present dataset, *Aquilapollenites* spp., *Complexiopollis* spp. and *Wodehouseia spinata* are widespread in Cretaceous sediments (Funkhouser, 1961; Drew and Tschudy, 1968; Tschudy, 1973b; Frederiksen, 1987, 1989; Johnson et al., 1989; Cross and Phillips, 1990), and Palaeogene examples are frequently counted as reworked (Fairchild and Elsik, 1969; Srivastava, 1994; Elsik and Yancey, 2000). However, these were included in the analyses that follow for a number of reasons. First, relatively little has been published on the Cretaceous palynology of the GCP, and so it is not possible to

say with certainty what is typical of the older sediments compared to those in the Palaeogene. Second, specimens assignable to *Complexiopollis* were relatively widespread and did not correspond exactly to forms described from the Cretaceous of the GCP (see Appendix 1), suggesting that these may represent previously undescribed taxa that were produced by plants that were present on the GCP during the Palaeogene. Third, preservation of both *Complexiopollis* and *Aquilapollenites* types was frequently excellent, reducing the likelihood of exposure and redeposition. Fourth, certain species of *Aquilapollenites* and *Wodehouseia* are thought to have lingered on into the Paleocene (Frederiksen, 1994a; Jarzen and Nichols, 1996), and so it is far from certain if Paleocene occurrences of those genera definitely are instances of reworking. Fifth, aside from *Complexiopollis* spp. and *Aquilapollenites attenuatus*, all other occurrences of these taxa are as singletons, which means that they are not included in several of the analyses anyway (i.e. NMDS [Chapters 5 to 7], ADP [Chapter 6], and the turnover tabulations [Chapter 7]). Carrying out all analyses with these taxa removed did not qualitatively alter the results, and so those presented in this thesis are for the entire dataset.

CHAPTER 4: SYSTEMATICS

This chapter includes systematic descriptions of all morphotypes that have not been found in the studied palynological literature. These taxa have been assigned informal names based on likely form genus membership. Systematic information for morphotypes that have been previously described in the literature is provided in Appendix 1. Taxa that were informally described in Jardine and Harrington (2008), and that have not since been synonymised with existing morphotypes, have been re-described, often with reference to specimens found in more recently counted samples. The taxon descriptions are arranged by major morphological group (e.g. Trilete isosporites, Tricolporate pollen), and then alphabetically by form genus and form species. I have followed the style used by *Palynology* for the format of taxon names and synonymy lists. Terminology follows Punt et al. (2007).

TRILETE ISOSPORES

Genus *Camarozonosporites* Pant 1954 ex Potonié 1956 emend. Klaus 1960

Type species. *Camarozonosporites cretaceus* (Weyland & Krieger 1953) Potonié 1956.

Remarks. *Camarozonosporites* describes trilete spores with rugulate sculpture on the distal exine, and smooth proximal exine. The laesurae reach the equator, and the amb is well rounded with convexly curved sides, which are enhanced by inter-radial crassitudes. This latter feature distinguishes *Camarozonosporites* from *Hamulatisporis*

Krutzsch 1959 emend. Srivastava 1972, which lacks inter-radial crassitudes. The genus *Inundatisporis* (Krutzsch 1963) Srivastava 1972 has a proximal sculpture, which *Camarozonosporites* lacks (Srivastava, 1972).

Camarozonosporites sp.1

Plate 1, figure 13

Camarozonosporites sp. Jardine and Harrington, 2008, pl. 1, fig. 8.

Description. Trilete microspore; amb subcircular; laesurae long, almost reach equatorial margin; inter-radial crassitudes 3 μm thick at their widest point; proximal face psilate; distal face rugulate; rugulae 1.5 – 2 μm wide, angular in shape, lumina 2 – 5 μm wide.

Dimensions. Equatorial diameter 60 μm (one specimen measured).

Remarks. This morphotype is characterised by its large size and relatively fine sculpture. It is much larger than *Camarozonosporites grootii*, and has narrower, shorter, less winding and more angular rugulae. The inter-radial crassitudes are also thinner on this morphotype than on *Camarozonosporites grootii*.

Affinity. Probably Lycopodiaceae (Srivastava, 1972).

Occurrence. One specimen recorded in the uppermost Nanafalia Formation on the eastern Gulf Coast.

Trilete spore, clavate

Plate 2, figures 14-15

Description. Trilete microspore; amb obtuse-straight-triangular to obtuse-concave-triangular; laesurae $1/2$ to $2/3$ radius of spore in length; exine $1\text{ }\mu\text{m}$ thick; spore densely covered in elements $1 - 3\text{ }\mu\text{m}$ high, variously club-shaped (clavae) or with tapering ends.

Dimensions. Equatorial diameter $26 - 33\text{ }\mu\text{m}$ (two specimens measured).

Remarks. This taxon is characterised by its sculpture of densely packed, free-standing clavae and bacula. I have not assigned this species to *Baculatisporites* because that genus includes spores with more or less circular amb, and this taxon has a distinctly triangular amb.

Affinity. The sculpture on this taxon suggests a possible affinity with Osmundaceae (Kruttsch et al., 1967).

Occurrence. Two specimens recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Trilete spore, reticulate

Plate 2, figure 16

Description. Trilete microspore; amb convex-triangular; laesurae $2/3$ radius of spore in length; exine $1.5\text{ }\mu\text{m}$ thick on sides of amb, thickens to $2\text{ }\mu\text{m}$ at grain angles;

sculpture reticulate to retistriate, lumina 0.5 – 1 μm wide, muri ~0.3 μm wide.

Dimensions. Equatorial diameter 21 μm (one specimen measured).

Remarks. The single grain of this type encountered is compressed and so exact details of shape are hard to discern. Similarly it is hard to determine if the sculpture is retistriate or if this is just a product of the muri being pressed together over some parts of the grain. On uncompressed areas some of the muri do appear to run parallel to one another, suggesting that this taxon might be weakly retistriate. It differs from other reticulate spores in its small size and fine reticulum.

Affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Trilete spore, verrucate

Plate 2, figure 17

Description. Trilete microspore; amb obtuse-concave-triangular; laesurae 2/3 to 3/4 radius of spore in length; exine 1 μm thick, verrucate, verrucae 1 – 2 μm wide and <0.5 μm high.

Dimensions. Equatorial diameter 26 – 34 μm (two specimens measured).

Remarks. This taxon is characterised by its verrucate sculpture. *Stereisporites granistereoides* is smaller and has a convex-triangular amb. *Polypodiisporonites* is monolete.

Affinity. Unknown.

Occurrence. Three specimens recorded in the Tusahoma Formation on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

ZONOPORATE POLLEN

Genus *Compositoipollenites* Potonié 1951 ex Potonié 1960

Type species. *Compositoipollenites rhizophorus* (Potonié 1934) Potonié 1951 ex Potonié 1960.

Remarks. This genus includes spheroidal pollen with an echinate sculpture. The type species has echinae 3 – 4 μm long, which are rose-thorn-like in appearance. The pores are indistinct, and colpi may be present. This genus differs from *Malvacipollis* in having larger, more thorn-like echinae.

Compositoipollenites sp. 1

Plate 5, figure 19

Description. Monad pollen, radial, isopolar, spheroidal; pores indistinct but probably tetraporate, pores endannulate, circular, 2 μm in diameter, endannuli 6 μm in diameter; exine 1 μm thick, sexine:nexine ratio 2:1, sexine columellate; sculpture comprises loosely spaced supratectal echinae 2 – 3 μm long and 1 μm wide at the base, sharply pointed, negative reticulum lacking; surface between the echinae finely granulate.

Dimensions. Greatest dimension (not including echinae) 22 μm (one specimen measured).

Remarks. This specimen is orientated in equatorial view and the pores are hard to make out amongst the echinae. However, there do appear to be four pores, rather than the more usual three for this genus. The echinae are long and ‘thorn’-like, and so I have placed this specimen in *Compositoipollenites* rather than *Malvacipollis*. *Compositoipollenites* sp. 2 has six pores and is more densely echinate; *Compositoipollenites grandianulatus* Frederiksen in Frederiksen et al. 1983 is triporate.

Affinity. Frederiksen (in Frederiksen et al., 1983) considered Sterculioideae of the Malvaceae s.l., Icacinaceae, and Euphorbiaceae as being possible parent plant families/subfamilies for similar pollen morphotypes.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Compositoipollenites sp. 2

Plate 5, figure 20

Description. Monad pollen, radial, isopolar, spheroidal; hexaporate, pores endannulate, circular, 3 μm in diameter, endannuli 6 μm in diameter and 1.5 μm thick; exine 1.8 μm thick, sexine:nexine ratio 2:1, columellae indistinct; supratectal echinae 3 μm long and 1 – 1.5 μm wide at the base, sharply pointed, negative reticulum lacking; surface between the echinae finely granulate.

Dimensions. Equatorial diameter (not including echinae) 21 μm (one specimen

measured).

Remarks. This morphotype is distinguished by the presence of six pores, rather than the three that are usual for this genus. *Compositoipollenites* sp. 1 differs in being tetraporate, less densely echinate, and more distinctly columellate.

Compositoipollenites grandiannullatus Frederiksen in Frederiksen et al. 1983 is triporate.

Affinity. Frederiksen (in Frederiksen et al., 1983) considered Sterculioideae of the Malvaceae *s.l.*, Icacinaceae, and Euphorbiaceae as being possible parent plant families/subfamilies for similar pollen morphotypes.

Occurrence. One specimen recorded in the Meridian Sand Member of the Tallahatta Formation on the eastern Gulf Coast.

TRICOLPATE POLLEN

Genus *Foveotricolpites* Pierce 1961

Type species. *Foveotricolpites sphaeroides* Pierce 1961.

Remarks. *Foveotricolpites* accommodates pollen that is tricolpate and foveolate. *Fraxinoipollenites*, *Rousea*, *Retitrescolpites* and *Tricolpites* differ in being reticulate.

Foveotricolpites sp. 1

Plate 7, figure 6

Description. Monad pollen, radial, isopolar, amb convex-triangular to circular but

deeply incised by the colpi; tricolpate, colpi gaping, extend almost to poles, thin costae 0.5 μm wide present along edges of colpi, thickened margins absent; exine 1.5 μm thick, sexine:nexine ratio 1:1; sexine appears structureless in optical section; sexine foveolate, foveolae up to 1.5 μm wide on mesocolpia, fine to <0.5 μm wide on apocolpia and towards colpi margins, foveolae up to 2 μm apart from one another.

Dimensions. Equatorial diameter 52 μm (one specimen measured).

Remarks. This specimen is characterised by its large size and large, gaping colpi.

Foveotricolpites prolatus Frederiksen 1983 is distinctly prolate, and has a much finer ornamentation. *Rousea* is reticulate rather than foveolate.

Affinity. Unknown.

Occurrence. One specimen recorded in the Zilpha Formation on the eastern Gulf Coast.

Genus *Fraxinoipollenites* Potonié 1951 ex Potonié 1960

Type species. *Fraxinoipollenites pudicus* (Potonié 1934) Potonié 1951 ex Potonié 1960.

Remarks. *Fraxinoipollenites* accommodates prolate, tricolpate pollen with granulate to finely reticulate pollen. *Tricolpites* differs in including more or less spheroidal tricolpate pollen, but is otherwise similar.

Fraxinoipollenites sp. 1

Plate 7, figure 7

Description. Monad pollen, radial, isopolar, prolate; tricolpate, colpi extend almost to the poles, bordered by costae ~0.5 μm wide; exine 1 μm thick, sexine:nexine ratio 2.5:1; sexine distinctly columellate, semi-ectate, muri-clavate microreticulate, lumina <0.5 μm wide, muri <0.5 μm wide.

Dimensions. Polar diameter 36 μm ; equatorial diameter 21 μm (one specimen measured).

Remarks. *Fraxinopollenites medius* Frederiksen 1973 is similar to this taxon; the two may be conspecific. Specimens assigned to *Fraxinopollenites* spp. Frederiksen 1980 have a coarser reticulation.

Affinity. Unknown.

Occurrence. One specimen recorded in the Tuscaloosa Formation on the eastern Gulf Coast.

Genus *Retitrescolpites* Sah 1967

Type species. *Retitrescolpites typicus* Sah 1967.

Remarks. *Retitrescolpites* accommodates oblate to spheroidal tricolpate pollen with a coarsely reticulate to retipilate exine. *Tricolpites* and *Platanus* differ in being microreticulate, and *Rousea* differs in having a reticulum that fines towards the colpi and apocolpium.

Retitrescolpites sp. 1

Plate 7, figures 12-13

Description. Monad pollen, radial, isopolar, prolate; tricolpate, colpi boat-shaped, extend 1/2 way to the poles, 3 μm wide at equator, bordered by thickened margins that are 3 μm wide at equator and thin to points at ends of colpi; exine 2.5 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-ectate, muri-clavate reticulate, heterobrochate, lumina angular, 2 – 3 μm wide, muri simplibaculate, 0.3 μm wide.

Dimensions. Equatorial diameter 28 μm (one specimen measured)

Remarks. *Retitrescolpites anguloluminosus* has longer colpi that gape open, and a thinner exine. “*Retitrescolpites* sp. 1” Frederiksen in Frederiksen et al. 1983 is much larger and has a coarser reticulum.

Affinity. Unknown.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Genus *Rousea* Srivastava 1969

Type species. *Rousea subtilis* Srivastava 1969.

Remarks. *Rousea* includes tricolpate pollen that is reticulate and heterobrochate, with larger lumina on the mesocolpia than on the apocolpia and near the colpi margins. *Tricolpites* differs in being microreticulate and homobrochate; *Retitrescolpites* and *Fraxinoipollenites* are both homobrochate. *Bombacacidites* has larger lumina on the

apocolpia, and is tricolporate.

Rousea sp. 1

Plate 7, figure 15

Description. Monad pollen, radial, isopolar, prolate; tricolpate, colpi almost reach the poles, bordered by thickened margins 1.5 μm wide; exine 2 μm thick, sexine:nexine ratio 2:1; sexine columellate, semi-ectate, muri-clavate reticulate, lumina polygonal to longitudinally elongate, up to 2 μm wide on mesocolpia, <0.5 μm near colpi, muri 0.5 μm wide, duplibaculate.

Dimensions. Polar diameter 34 μm ; equatorial diameter 23 μm (one specimen measured).

Remarks. *Rousea crassimurina* Pocknall & Nichols 1996 is also duplibaculate, but has thicker muri (1 μm), is smaller in size, and has more rounded poles.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Genus *Striatopollis* Krutzsch 1959

Type species. *Striatopollis sarstedtensis* Krutzsch 1959.

Remarks. This genus includes prolate, tricolpate pollen with a striate exine ornamentation. *Aceripollenites* Nagy 1969 differs in being retistriate.

?*Striatopollis* sp. 1

Plate 7, figure 16

Description. Monad pollen, radial, isopolar, prolate; tricolpate, colpi almost reach the poles, unbordered, edges tightly appressed; exine 1 μm thick, sexine:nexine ratio 1:1, both sexine and nexine internally structureless; sexine striate, striae aligned parallel to the polar axis, some bifurcate, 0.5 μm wide, spaced 0.5 μm apart.

Dimensions. Polar diameter 31 μm ; equatorial diameter 21 μm (one specimen measured).

Remarks. This grain is in a poor state of preservation and split open, and precise details of the colpi are hard to determine. *Striatopollis tectatus* Leffingwell 1971 is tectate and columellate, and *Striatopollis terasmaei* (Rouse 1962) Frederiksen 1980 has geniculate colpi.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Genus *Tricolpites* Cookson 1947 ex Couper 1953 emend. Potonié 1960

Type species. *Tricolpites reticulatus* Cookson 1947 ex Couper 1953.

Remarks. *Tricolpites* includes oblate to spheroidal, tricolpate, trilobate pollen with a microreticulate exine. It differs from *Retitrescolpites* in having a finer reticulum, and from *Fraxinoipollenites* in including spheroidal, rather than prolate, pollen.

Tricolpites sp. 1

Plate 7, figure 21

Description. Monad pollen, radial, isopolar, amb straight-triangular with grain angles intersected by gaping colpi; tricolpate, colpi extend 1/2 way to poles, bordered by thickenings 0.5 μm wide, edges ragged, colpi 10 – 13 μm wide at equator; exine 1 μm thick between colpi, thins to 0.5 μm thick at colpi margins, caused by thinning of sexine; sexine columellate and tectate, punctate-microreticulate, lumina and muri 0.5 μm wide.

Dimensions. Equatorial diameter 28 – 29 μm (two specimens measured).

Remarks. This species differs from *Tricolpites hians* in having ragged edges to the colpi margins, from *Tricolpites asper* in being larger and having a more straight-sided amb, and from *Tricolpites* sp. 2 in having a finer reticulum and a more straight-sided amb.

Affinity. Unknown.

Occurrence. Four specimens recorded in the Calvert Bluff Formation in Texas.

Tricolpites sp. 2

Plate 7, figures 22-25

Tricolpites sp. cf. *T. asper*. Harrington, 2003b, pl. 1, fig. 26.

Description. Monad pollen, radial, isopolar, grain prolate spheroidal to \pm oblate in

shape, amb convex-triangular to subcircular to trilobate; tricolpate, colpi gaping open in polar view and deeply incised, extend 2/3 to 3/4 of the way to the poles, bordered by thickened margins 1 μm wide, edges of colpi often more or less ragged; exine 1 – 1.5 μm thick, sexine:nexine ratio 3:1; sexine columellate and semitectate, muri-clavate reticulate, lumina typically 0.5 – 1 μm wide, up to 2 μm wide on some specimens, heterobrochate across grain, muri 0.2 – 0.3 μm wide.

Dimensions. Polar diameter 19 – 31 μm , mean 26 μm (six specimens measured); equatorial diameter 22 – 38 μm , mean 29 μm (14 specimens measured).

Remarks. This taxon is characterised by its ragged colpi edges and very thin muri.

Platanus occidentaloides is similar in many respects, but differs in having a finer reticulum (lumina <0.5 μm). *Tricolpites* sp. 1 differs in amb shape and in having a much finer reticulum. *Retitrescolpites anguloluminosus* is similar in having very thin muri, but lacks ragged colpi margins, and typically has wider lumina (~2 μm).

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <5% in 18/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast.

Tricolpites sp. 3

Plate 7, figure 26; plate 8, figure 1

Description. Monad pollen, radial, isopolar, grain prolate to subprolate in shape; tricolpate, colpi almost reach the poles, only lightly bordered by thickenings; exine 1 – 2 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-ectate, muri-clavate

reticulate, lumina 0.5 – 1.3 μm wide, heterobrochate; muri 0.3 – 0.5 μm wide, simplibaculate.

Dimensions. Polar diameter 34 – 39 μm , mean 37 μm ; equatorial diameter 23 – 30 μm , mean 27 μm (four specimens measured).

Remarks. This taxon accommodates prolate to subprolate, muri-clavate reticulate tricolpate grains. The grains are variable in terms of exine thickness and lumina diameter, but are so similar in other respects that counting them separately did not seem worthwhile. *Fraxinoipollenites* sp. 1 is more distinctly prolate and has a finer reticulation style. *Fraxinoipollenites* spp. Frederiksen 1980 includes similar forms.

Affinity. Unknown.

Occurrence. Four specimens recorded in the Nanafalia, Tusahoma and Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Tricolpites sp. 4

Plate 8, figures 2-3

Description. Monad pollen, radial, isopolar, grain subprolate to spheroidal in shape, amb \pm circular; tricolpate, colpi extend 3/4 the way to the poles, typically unbordered but light thickened margins <1 μm wide sometimes present, appear narrow in equatorial view but gape open in polar view; exine 1.5 – 2 μm thick, sexine:nexine ratio 3:1; sexine pilate, pila loosely fused together to form a retipilate sculpture, lumina 0.5 – 1 μm wide, muri ~0.3 μm wide.

Dimensions. Polar diameter 23 – 27 μm , mean 25 μm ; equatorial diameter measured

in equatorial view 19 – 22 μm , mean 21 μm (four specimens measured); equatorial diameter measured in polar view 29 – 31 μm (two specimens measured).

Remarks. This taxon is characterised by its retipilate sculpture. *Favitricolporites baculoferus* has a similar sculpture but is tricolporate. Other reticulate tricolpate pollen types in this study are muri-clavate reticulate rather than retipilate.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <0.3% in 6/151 samples, from the Tuscaloosa to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Tricolpites sp. 5

Plate 8, figure 4

Description. Monad pollen, radial, isopolar, amb circular; tricolpate, colpi extend ~2/3 of way to poles, unbordered, open and deeply incised; exine 1.5 μm thick, nexine indistinct; sexine columellate, semi-tectate, muri-clavate reticulate, lumina ~1 μm in diameter, homobrochate, muri 0.6 μm wide, simplibaculate.

Dimensions. Equatorial diameter 45 μm (one specimen measured).

Remarks. The single grain found of this type is differentiated from the other tricolpate pollen in this study by its large size, spheroidal to oblate shape, and very thin nexine. “*Retitrescolpites* sp. 1” of Frederiksen in Frederiksen et al. 1983 has lumina 2 – 3 μm wide, and shorter colpi.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Genus *Tricolpopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type species. *Tricolpopollenites parmularius* Thomson & Pflug 1953.

Remarks. This is a generalised genus that includes spheroidal to prolate tricolpate pollen of variable exine ornamentation. Whilst the use of such a broad genus is generally rejected in favour of more restricted diagnoses, this genus is useful for accommodating tricolpate morphotypes that do not fit well into other form genera.

Tricolpopollenites sp. 1

Plate 8, figure 7

Description. Monad pollen, radial, isopolar, amb convex-triangular; tricolpate, colpi almost extend to poles, grain split and so appears syncolpate, colpi ~7 µm wide at equator, bordered by costae 1 µm wide; exine 1 µm thick, nexine indistinct and very thin, sexine gemmate, gemmae 1 µm high and 0.5 – 1 µm wide, size decreases towards colpi margins, loosely and heterogeneously cover grain, in places two or three gemmae coalesce.

Dimensions. Equatorial diameter 31 µm (one specimen measured).

Remarks. This specimen is distinguished from the other tricolpate morphotypes in this dataset by its gemmate ornamentation.

Affinity. Unknown.

Occurrence. One specimen recorded in the Meridian Sand Member of the Tallahatta Formation on the eastern Gulf Coast.

ZONOCOLPATE POLLEN

Pentacolpate pollen sp. 1

Plate 8, figures 8-9

Description. Monad pollen, radial, isopolar, amb convex-pentagonal; pentacolpate, colpi reach $1/2 - 2/3$ the way to the poles, lightly bordered by thickenings $<0.5\ \mu\text{m}$ wide; exine $1\ \mu\text{m}$ thick on one specimen, $1.5\ \mu\text{m}$ thick on the other, mesocolpial sexine:nexine ratio $\sim 2:1$ in both cases, sexine thins towards colpi so that at the colpi margins the sexine:nexine ratio is $\sim 1:1$; sexine finely columellate and tectate, surface of tectum smooth to very finely scabrate.

Dimensions. Equatorial diameter $33 - 34\ \mu\text{m}$ (two specimens measured).

Remarks. This taxon is the only one possessing five colpi within this dataset.

Pentacolporate pollen sp. 1 has ora as well as colpi and has a microechinate surface sculpture.

Affinity. Unknown. Pollen of *Nothofagus* Blume, and its associated form genus *Nothofagacidites* Potonié 1960, are similar to this specimen, but differ in being ornamented with microechinae and in having thickened colpi margins.

Occurrence. Two specimens recorded in the Calvert Bluff Formation in Texas.

TRICOLPORATE POLLEN

Genus *Araliaceoipollenites* Potonié 1951 ex. Potonié 1960

Type species. *Araliaceoipollenites euphorii* (Potonié 1931) Potonié 1951 ex. Potonié 1960.

Remarks. This genus incorporates tricolporate pollen with a columellate and granulate exine. It therefore differs from *Rhoipites*, *Horniella* and *Caprifoliipites*, which are reticulate, *Siltaria*, which is scabrate, and *Nyssapollenites*, which is punctate.

Araliaceoipollenites sp. 1

Plate 8, figure 15

Description. Monad pollen, radial, isopolar, grain prolate in shape; tricolporate, colpi extend almost to poles, bordered by thickened margins 1.5 μm wide; ectopore poorly developed, endopore distinct circular, 4 μm in diameter, unbordered; exine 2.5 μm thick at equator, 3 μm thick at poles, nexine 1 μm thick throughout, increase in thickness at poles caused by increase in sexine thickness; sexine indistinctly columellate in equatorial region, \pm internally structureless at poles, surface finely granulate, more obviously so near the equator than at the poles.

Dimensions. Polar diameter 33 μm ; equatorial diameter 24 μm (one specimen measured)

Remarks. This taxon has a very thick sexine that is thicker at the poles than at the

equator, and only (indistinctly) columellate in the equatorial area. *Nuxpollenites* has thicker exine at the poles than at the equator, but this is caused by the presence of a columellate endosexine that is restricted to the poles. I have tentatively placed this taxon in *Araliaceoipollenites* because the surface appears granulate. *Araliaceoipollenites megaporifer* Frederiksen 1980 is more distinctly columellate and granulate and has a thinner exine, but is otherwise similar.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Genus *Caprifoliipites* Wodehouse 1933

Type species. *Caprifoliipites viridifluminis* Wodehouse 1933.

Remarks. This genus includes prolate to spheroidal, tricolporate reticulate grains with indistinct ora. *Caprifoliipites* is most similar to *Horniella*, but differs from this, and other reticulate tricolporate genera, in having indistinct rather than distinct ora.

Caprifoliipites sp. 1

Plate 8, figure 22

Description. Monad pollen, radial, isopolar, grain subprolate in shape; tricolporate, colpi long, almost reach poles, costate, costae ~0.5 µm wide; ora indistinct and unbordered, expressed as gaps in colpi 9 µm long, presumably very lologate; exine 2 µm thick, sexine:nexine ratio 3:1; sexine columellate, semi-tectate, muri-clavate

microreticulate, \pm homobrochate, lumina 0.4 – 0.6 μm wide, muri 0.2 – 0.5 μm wide, simplibaculate.

Dimensions. Polar diameter 33 μm ; equatorial diameter 26 μm (one specimen measured).

Remarks. This taxon is characterised by its lolongate ora and fine reticulum.

Caprifoliipites sp. 2 is smaller and has \pm circular ora, and *Caprifoliipites* sp. 3, 4 and 5 are more coarsely reticulate. *Caprifoliipites incertigrandis* Frederiksen 1980 is more coarsely reticulate and has circular to lalongate ora.

Affinity. Unknown.

Occurrence. One specimen recorded in the Zilpha Formation on the eastern Gulf Coast.

Caprifoliipites sp. 2

Plate 8, figure 23

Description. Monad pollen, radial, isopolar, grain subprolate in shape; tricolporate, colpi almost reach poles, lightly bordered by thickenings 0.5 μm wide; ora indistinct and unbordered, expressed as gaps in colpi, probably circular to slightly lolongate, exine 1 – 1.3 μm thick, sexine:nexine ratio 2:1; sexine columellate, semi-tectate, muriclavate microreticulate to almost punctate in some specimens, homobrochate, lumina 0.3 μm wide, muri 0.2 – 0.5 μm wide.

Dimensions. Polar diameter 23 – 24 μm , mean 23 μm ; equatorial diameter 18 – 21 μm , mean 19 μm (four specimens measured).

Remarks. This taxon differs from *Caprifoliipites* sp. 1 in being smaller and more finely reticulate. *Caprifoliipites* sp. 3, 4 and 5 are much more coarsely reticulate.

Affinity. Unknown.

Occurrence. Seven specimens recorded in sample SM/08/001 from the Calvert Bluff Formation in Texas.

Caprifoliipites sp. 3

Plate 8, figure 24

Description. Monad pollen, radial, isopolar, grain prolate in shape; tricolporate, colpi long, almost reach the poles, bordered by thickenings ~0.3 µm wide; ora indistinct and unbordered, appear as breaks in the colpi, presumably distinctly lolongate; exine 1.5 µm thick, sexine:nexine ratio 3:1; nexine punctate; sexine columellate, semi-tectate, reticulate, heterobrochate, lumina irregular in shape, 2 – 5 µm in greatest dimension, muri 0.3 µm wide, simplibaculate.

Dimensions. Polar diameter 31 µm; equatorial diameter 21 µm.

Remarks. This taxon is characterised by its distinctive reticulation style with wide lumina and very thin muri, and distinctly lolongate, indistinct ora. *Caprifoliipites* sp. 4 is superficially similar but is muri-clavate reticulate and has more distinct ora. *Caprifoliipites* sp. 1 has a much finer muri-clavate reticulum.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Caprifoliipites sp. 4

Plate 8, figures 25-26

Description. Monad pollen, radial, isopolar, grain prolate in shape; tricolporate, colpi long, almost reach poles, bordered by thickenings 1 μm wide; ora distinctly lologate, 2 μm wide by 10 μm long, unbordered; exine 2 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-tectate, muri-clavate reticulate, heterobrochate, lumina irregular in shape, 2 – 5 μm in greatest dimension, muri 0.5 μm wide, simplibaculate.

Dimensions. Polar diameter 33 μm ; equatorial diameter 20 μm .

Remarks. *Caprifoliipites* sp. 4 is similar in many respects to *Caprifoliipites* sp. 3, especially in terms of the style of reticulation. It differs in having more distinct ora and in having columellae that are clavate in optical section.

Affinity. Unknown.

Occurrence. One specimen recorded in the Tallahatta Formation on the eastern Gulf Coast.

Caprifoliipites sp. 5

Plate 8, figure 27; plate 9, figure 1

Description. Monad pollen, radial, isopolar, grain prolate in shape; tricolporate, colpi long, almost reach poles, bordered by thickenings 1 μm wide, flare out slightly at ora; ora indistinct, appear as breaks in colpi 10 – 12 μm long, presumably very

lolongate; exine 2.5 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-tectate, muri-clavate reticulate, heterobrochate, lumina 1 – 2 μm wide, muri 0.7 μm thick, simplibaculate.

Dimensions. Polar diameter 39 – 40 μm ; equatorial diameter 25 – 28 μm (two specimens measured).

Remarks. This morphotype shares with *Caprifoliipites* sp. 1, 3 and 4 distinctly lolongate ora, but differs in being more coarsely reticulate than *Caprifoliipites* sp. 1, and having smaller lumina and wider muri than *Caprifoliipites* sp. 3 and 4.

Affinity. Unknown.

Occurrence. Two specimens recorded in the Naheola and Nanafalia formations on the eastern Gulf Coast.

Genus *Favitricolporites* Sah 1967 emend. Srivastava 1972

Type species. *Favitricolporites eminens* Sah 1967.

Remarks. As emended by Srivastava (1972), *Favitricolporites* includes tricolporate pollen with a retipilate sculpture (i.e., comprising pila or clavae that are partially fused together into a reticulum). The amb shape can vary from triangular to circular, and the grain is subprolate to spheroidal. The presence of a retipilate sculpture distinguishes *Favitricolporites* from *Ilexpollenites*, in which the pilae or clavae are free standing, and *Rhoipites* and *Horniella*, which are truly reticulate.

Favitricolporites sp. 1

Plate 9, figure 12

Description. Monad pollen, radial, isopolar, grain spheroidal to prolate spheroidal in shape; tricolporate, colpi extend $\sim 3/4$ of way to poles, lightly bordered by thickenings in some specimens, the colpi on some grains are also geniculate; ora unbordered and somewhat indistinct, circular to lalongate and elliptical, 2 – 4 μm wide by 1 – 2 μm high; exine ~ 1.5 μm thick, sexine:nexine ratio 2 – 3:1; sexine retipilate, heads of pila fused into loose microreticulum, lumina and muri < 0.5 μm wide.

Dimensions. Polar diameter 19 – 24 μm , mean 22 μm ; equatorial diameter 19 – 23 μm , mean 21 μm (four specimens measured).

Remarks. This taxon is heterogeneous, but represents small, spherical, retipilate tricolporate pollen grains. *Favitricolporites baculoferus* is larger and has a coarser retipilum, and *Favitricolporites* sp. 2 has more distinct ora and a coarser retipilum. *Tricolpites* sp. 4 is tricolpate rather than tricolporate.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of $< 1\%$ in 5/151 samples, in the Hatchetigbee and Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Favitricolporites sp. 2

Plate 9, figure 13

Description. Monad pollen, radial, isopolar, grain spheroidal in shape; tricolporate, colpi almost reach poles, unbordered; ora distinct, circular, 3 μm in diameter, endannulus 4 μm wide; exine 2 μm thick at equator, thins to 1 μm thick at poles, nexine 0.5 μm thick throughout, difference in exine thickness caused by sexine thinning towards poles; sexine retipilate, heads of pila fused into loose microreticulum, heterobrochate, lumina 0.5 – 1.5 μm wide, muri 0.3 μm wide.

Dimensions. Polar diameter 23 μm ; equatorial diameter 23 μm (one specimen measured).

Remarks. This taxon has larger lumina and more distinct ora than either

Favitricolporites baculoferus or *Favitricolporites* sp. 1. “*Favitricolporites* sp. 1”

Frederiksen in Frederiksen et al. 1983 is very similar but is smaller (16 – 17 μm) and has a thinner exine.

Affinity. Unknown.

Occurrence. Two specimens recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Favitricolporites sp. 3

Plate 9, figures 14-15

Tricolporopollenites sp. 8. Jardine and Harrington, 2008, p. 199, pl. 4, fig. 8.

Description. Monad pollen, radial, isopolar, amb \pm circular; tricolporate, colpi almost reach poles, bordered by thickenings 2 μm wide; ora circular, possibly endannulate;

exine 2 μm , sexine:nexine ratio 4:1; sexine microreticulate, densely columellate, hard to determine if rods are clavae or pila in optical section, difference in width between columellae and capita only slight, almost bacula; reticulum heterobrochate, lumina <0.5 μm wide, muri ~0.3 μm wide.

Dimensions. Equatorial diameter 27 – 29 μm (two specimens measured).

Remarks. *Favitricolporites* sp. 3 is distinguished from other *Favitricolporites* types by its thin pila that are densely distributed over the grain, and by its long and thickened colpi.

Affinity. Unknown.

Occurrence. Three specimens recorded in the Tusahoma Formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Horniella* Traverse 1955

Type species. *Horniella clavaticosta* Traverse 1955.

Remarks. *Horniella* includes prolate to spheroidal grains with distinct lalongate to round ora, long, unbordered or lightly bordered colpi, and a reticulate ornamentation with high muri. *Caprifoliipites* differs in having obscure ora, and *Rhoipites* differs in having thickened margins bordering the colpi.

Horniella sp. 1

Plate 9, figure 21

Description. Monad pollen, radial, isopolar, prolate; tricolporate, colpi almost reach the poles, ~1 μm wide, bordered by costae 1.5 μm wide; ora circular, 4 μm in diameter; exine 2 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-tectate, muri-clavate microreticulate, \pm homobrochate, lumina ~0.5 μm wide, muri about the same or slightly thinner.

Dimensions. Polar diameter 39 μm ; equatorial diameter 21 μm (one specimen measured).

Remarks. *Horniella brevicolpata* is larger, has relatively shorter colpi, and a coarser, retistriate ornamentation. *Horniella* sp. 2 and 3 are more spheroidal and have coarser reticula.

Affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Horniella sp. 2

Plate 9, figures 22-23

Description. Monad pollen, radial, isopolar, subprolate; tricolporate, colpi almost reach poles, 2 μm wide, thinly bordered by nexinal thickenings that flare out at ora; ora large, unbordered, slightly lalongate, 7 μm wide by 5 μm high; exine 2 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-tectate, muri-clavate reticulate, reticulum heterobrochate, lumina 1 – 3 μm wide, irregular in shape, muri simplibaculate, 0.5 μm wide.

Dimensions. Polar diameter 36 μm ; equatorial diameter 28 μm (one specimen measured).

Remarks. *Horniella* sp. 2 is distinguished by its large, indistinct ora and coarse reticulum with relatively thin muri. *Horniella* sp. 3 has distinctly lalongate ora, a more spheroidal shape, and thicker simpli- to duplibaculate muri.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Horniella sp. 3

Plate 9, figures 24-25

Description. Monad pollen, radial, isopolar, prolate spheroidal; tricolporate, colpi almost reach poles, costae colpi 1.5 μm wide, curve inwards towards colpi above and below ora; ora distinctly lalongate as defined by the curved ends of the costae colpi, otherwise ill-defined; exine 2 μm thick, sexine:nexine ratio 1.5:1; sexine columellate, semi-ectate, muri-clavate reticulate, reticulum heterobrochate, lumina <0.5 – 2 μm wide, muri simpli- to duplibaculate, 0.5 – 1 μm wide.

Dimensions. Polar diameter 31 μm ; equatorial diameter 30 μm (one specimen measured).

Remarks. *Horniella* sp. 2 differs in being subprolate, having a relatively thinner nexine, larger ora, wider lumina and narrower muri, and in being exclusively simplibaculate. *Rhoipites* sp. 3 differs in having larger, better-defined ora and more heavily thickened colpi.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Genus *Lanagiopollis* Morley 1982

Type species. *Lanagiopollis regularis* Morley 1982.

Remarks. This form genus includes large, oblate pollen with a circular to obtuse-convex-triangular amb. The colpi are wide but are not typically deeply incised; the length of the colpi and the presence and thickness of margins varies between species. The ora are typically large, and as wide as the colpi at the equator. The sexine is either reticulate or rugulate, and the muri may be either simplibaculate, duplibaculate or pluribaculate. Also variable between species is the sexine:nexine ratio, although the nexine often thins towards the apertures. This heterogeneous genus therefore includes reticulate or rugulate pollen of *Alangium* type (Cornaceae), and *Pelliceria* type (Theaceae) (Frederiksen, 1988). *Alangium* type pollen that is striate or retistriate is accommodated within *Alangiopollis* Krutzsch 1962 emend. Morley 1982. *Nyssapollenites* includes oblate tricolporate grains that are infrapunctate rather than reticulate or rugulate. *Rhoipites* and *Horniella* have a reticulate sculpture but are prolate to spheroidal in shape. *Margocolporites* Ramanujam 1966 ex. Srivastava 1969 is margocolporate; that is with three, broad colpus-like streaks of differentiated sexine, with small true colpi and ora at their centres. *Lanagiopollis* differs in having three wide colpi, which may or may not have thickened margins.

Lanagiopollis sp. 1

Plate 10, figure 16

Tricolporopollenites sp. 8. Jardine and Harrington, 2008, p. 199, pl. 4, fig. 3.

Description. Monad pollen, radial, isopolar, amb obtuse-convex-triangular; tricolporate, colpi 3 μm wide at equator, extend ~ 4 μm towards poles from equator; ora indistinct in plan view, surrounded by heavy endannuli 3 μm thick and ~ 12 μm wide; exine 2 μm thick at mesocolpia, 1 μm thick at colpi margin, caused by a thinning of both the sexine and the nexine; sexine columellate, semitectate, muriculate reticulate, heterobrochate, lumina 0.5 – 1 μm wide, muri simplibaculate, 0.5 – 1 μm wide, sculpture diminishes towards colpi, indistinct over endannuli.

Dimensions. Equatorial diameter 36 – 41 μm , mean 38 μm (three specimens measured).

Remarks. This species is similar to *Lanagiopollis* species erected by Morley (1982) from the Middle to Late Eocene of Southeast Asia, in being brevicolpate and heavily endannulate. Of these species *Lanagiopollis regularis* has a finer reticulum and a much thicker nexine; *Lanagiopollis microrugulatus* and *Lanagiopollis ruguloverrucatus* are both rugulate; and *Lanagiopollis nanggulanensis* is rugulate to reticulate and has margins that are distinctly thickened at the equator. All four species are also larger than *Lanagiopollis* sp.1, with equatorial diameters of 60 – 100 μm . Other *Lanagiopollis* species previously recorded on the Gulf Coast have longer colpi and do not possess such thick endannuli.

Affinity. Probably *Alangium* (Cornaceae) (Morley, 1982).

Occurrence. Three specimens recorded in the Tuscahoma Formation on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Lanagiopollis sp. 2

Plate 10, figures 17-18

Description. Monad pollen, radial, isopolar, prolate spheroidal; tricolporate, colpi almost reach poles, shallow, bordered by distinct, thickened margins 1 μm wide; ora slightly lalongate, 7 μm wide by 5 μm high; exine 3 μm thick, sexine:nexine ratio 1.5:1; sexine columellate, semi-tectate, muri-clavate reticulate, reticulum heterobrochate, lumina 1 – 3 μm wide, irregular in shape, muri simplibaculate, 0.5 μm wide.

Dimensions. Polar diameter 38 μm ; equatorial diameter 36 μm (one specimen measured).

Remarks. This specimen is very similar to *Lanagiopollis hadrodictya*, but differs in having less deeply incised colpi.

Affinity. Possibly Cornaceae.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Genus *Porocolpopollenites* Pflug in Thomson & Pflug 1953

Type species. *Porocolpopollenites vestibuloformis* Pflug in Thomson & Pflug 1953.

Remarks. This genus includes tri- to tetracolporate grains with distinct postvestibula. The exine may be sculptured or smooth, and the colpus is typically short but may be indistinct or entirely absent. The grains are oblate in shape. This form genus therefore includes pollen similar to that produced by extant *Symplocos*, and is probably at least referable to Symplocaceae (Frederiksen, 1988). *Symplocoipollenites* Potonié 1951 ex. Potonié 1960 also includes oblate, brevicolpate, vestibulate pollen, but according to the original diagnosis is limited to granulate to rugulate specimens. *Intratropopollenites* is also postvestibulate but this genus is planaperturate rather than angulaperturate.

Porocolpopollenites sp. 1

Plate 11, figure 9

Description. Monad pollen, radial, isopolar, amb obtuse-convex-triangular; angulaperturate, tricolporate, brevicolpate, colpi reach ~1/3 of way to poles, unbordered, 3 µm wide at equator but narrowing rapidly away from equator to become slit-like beyond the endannuli; ora postvestibulate, endannulate, endannuli ±semi-circular in shape, 1 µm thick, ectonexine and sexine only extend ~1 µm beyond the edge of the postvestibulum, postvestibulum ~3 µm deep; exine 1 µm thick, sexine:nexine ratio 2.5:1; sexine columellate, semi-tectate, muri-clavate reticulate,

heterobrochate, lumina are larger on apocolpium and fine towards mesocolpia, lumina up to 3 μm on apocolpia, ~ 1 μm on mesocolpia; muri 0.3 μm wide, simplibaculate.

Dimensions. Equatorial diameter 28 μm (one specimen measured).

Remarks. The specimen assigned to *Porocolpopollenites* sp. 1 possesses an unusual mix of morphological characters associated with different brevicolporate form genera. It is post-vestibulate and angulaperturate like *Porocolpopollenites*, but also heterobrochate with smaller lumina on the mesocolpia than apocolpia, like *Bombacacidites*. The aperture style is similar to *Intratropopollenites pseudinstructus*, but that species (and genus) is planaperturate.

Affinity. The brevicolporate, post-vestibulate nature of the apertures, and their positioning at the angles of the grain, suggest an affinity with *Symplocos* (Symplocaceae).

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Porocolpopollenites sp. 2

Plate 11, figure 10

Description. Monad pollen, radial, isopolar, amb obtuse-convex-triangular; tricolporate, colpi extend $\sim 3/4$ of the way to the poles, 3 – 4 μm wide at the equator, bordered by thickened margins 2 μm wide; ora vestibulate, vestibulum 8 μm wide and 2.5 μm deep, otherwise obscure; exine 2 μm thick, ectosexine:endosexine:nexine

ratio 3:1:1; endosexine columellate, outer surface of ectosexine rough in optical section, reticulate to rugulate in plan view, muri ~0.3 µm wide, lumina <2 µm wide.

Dimensions. Equatorial diameter 28 µm (one specimen measured).

Remarks. This grain is degraded and it is hard to make out the details of the ornamentation. It is distinguished by its long, bordered colpi, thin columellate layer (endosexine) and thick tectum (ectosexine). *Porocolpopollenites* sp. 1 has shorter colpi and a heterobrochate reticulum.

Affinity. Unknown.

Occurrence. One specimen recorded in the Tuscahoma Formation on the eastern Gulf Coast.

Porocolpopollenites sp. 3

Plate 11, figures 11-12

Porocolpopollenites spp. Elsik, 1968b, p. 634, pl. 28, figs. 13-14 only.

Tricolporopollenites sp. Harrington, 2003b, pl. 1, fig. 29.

Porocolpopollenites sp. Jardine and Harrington, 2008, pl. 3, fig. 18.

Description. Monad pollen, radial, isopolar, amb ±circular; tricolporate, colpi reach at least 3/4 of the way to the poles, narrow, ~1 µm wide at equator, bordered by broad thickened margins, 2 – 4 µm wide at equator, narrow to point at end of colpi; ora indistinct, vestibulate; exine 0.7 – 1 µm thick, nexine obscure, surface granulate.

Dimensions. Equatorial diameter 15 – 20 µm, mean 18 µm (three specimens

measured).

Remarks. This taxon includes small tricolporate pollen grains with vestibulate ora and relatively long colpi bordered by wide thickened margins. *Porocolpopollenites* sp. 1 and 2 are larger and have reticulate exines.

Affinity. Unknown.

Occurrence. Four specimens recorded in the Naheola and Tuscahoma formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Ranunculacidites* Sah 1967

Type species. *Ranunculacidites communis* Sah 1967.

Remarks. This genus includes oblate, tricolp(or)ate pollen with an operculum over the apertures. The exine ornamentation is variable. The presence of an operculum distinguished *Ranunculacidites* from other tricolpate to tricolporate form genera.

Ranunculacidites sp. 1

Plate 11, figure 13

Description. Monad pollen, radial, isopolar, amb convex-triangular; tricolporate, the colpi extend almost to the poles, edges ragged, bordered by costae ~0.5 μm wide, colpi ~6 μm wide at the equator; well-developed opercula present on all apertures, ora difficult to see but probably the same width as the colpi at the equator; exine 1 μm thick, sexine:nexine ratio 1:1; sexine finely granulate.

Dimensions. Equatorial diameter 25 μm (one specimen measured).

Remarks. *Ranunculacidites striatus* Frederiksen in Frederiksen et al. 1983 is finely striate, and *Ranunculacidites communis* Sah 1967 is finely reticulate.

Affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Genus *Rhoipites* Wodehouse 1933

Type species. *Rhoipites bradleyi* Wodehouse 1933.

Remarks. *Rhoipites* accommodates spheroidal to prolate, reticulate pollen grains with long, distinctly thickened colpi. *Lanagiopollis* includes reticulate grains that are spheroidal to oblate, *Horniella* includes reticulate grains with only lightly bordered colpi, *Ailanthipites* is foveo-striate, and *Caprifoliipites* is smaller and has indistinct ora.

Rhoipites sp. 1

Plate 11, figures 20-23

Rhoipites sp. 1. Jardine and Harrington, 2008, p. 196, pl. 3, fig. 20.

Description. Monad pollen, radial, isopolar, prolate to prolate spheroidal; tricolporate, colpi long, almost reach poles, lightly bordered by thickenings 0.5 – 1 μm wide, flare out at ora; ora large and lolongate, 4 – 6 x 6 – 10 μm wide,

±unbordered; exine 1 – 2 μm thick, sexine:nexine ratio 2 – 3:1; sexine columellate, semi-ectate, muri-clavate reticulate, heterobrochate, lumina 0.5 – 2 μm wide, polygonal to elongate in shape, muri simplibaculate, <0.8 μm (typically <0.5 μm) wide.

Dimensions. Polar diameter 35 – 45 μm , mean 39 μm ; equatorial diameter 22 – 30 μm , mean 26 μm (18 specimens measured).

Remarks. *Rhoipites* sp. 1 is similar in many respects to *Rhoipites cryptoporus*, but differs in its larger size, and in having larger, distinctly lolate ora. *Rhoipites latus* differs in having circular ora, longitudinally elongate lumina, and wide muri.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <2% in 26/151 samples, from the Naheola to the base of the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Rhoipites sp. 2

Plate 11, figure 24

Description. Monad pollen, radial, isopolar, subprolate; tricolporate, colpi long, almost reach poles, lightly bordered by thickenings ~0.5 μm wide; ora round, 3 μm wide, endannulate?; exine 2 μm thick, ectosexine:endosexine:nexine ratio 0.5:4:1; sexine columellate, semi-ectate, muri-clavate microreticulate, heterobrochate, lumina 0.5 – 1 μm wide, irregular in shape, muri simplibaculate, ~0.2 μm wide.

Dimensions. Polar diameter 30 μm ; equatorial diameter 24 μm (one specimen

measured).

Remarks. This specimen possesses very high and narrow muri. Other *Rhoipites* species do not have such a thick columellate layer (endosexine).

Affinity. Unknown.

Occurrence. One specimen recorded in the Tallahatta Formation on the eastern Gulf Coast.

Rhoipites sp. 3

Plate 11, figure 25

Description. Monad pollen, radial, isopolar, prolate spheroidal; tricolporate, colpi reach $\sim 2/3$ of the way to the poles, bordered by thickenings 2 μm wide at ora, narrow toward ends of colpi; ora \pm circular, $\sim 5 \mu\text{m}$ in diameter; exine 2 μm thick, sexine:nexine ratio 3:1; sexine columellate, semi-ectate, muri-clavate foveo-reticulate, heterobrochate, lumina 0.5 – 1.5 μm wide, muri polybaculate, 1 – 1.5 μm wide.

Dimensions. Polar diameter 35 μm ; equatorial diameter 31 μm (one specimen measured).

Remarks. This taxon is distinguished by its polybaculate foveo-reticulate sculpture, large ora and thickened colpi. I have placed it in *Rhoipites* because it is prolate spheroidal; if it were more oblate, *Lanagiopollis* would be a more suitable form genus. *Rhoipites capax* is also prolate spheroidal, but is more coarsely reticulate. Other species of *Rhoipites* in this dataset have narrower muri relative to the diameter of the lumina, and are more prolate.

Affinity. Unknown, although membership of Alangiaceae is not precluded.

Occurrence. Two specimens recorded in the Calvert Bluff Formation in Texas.

Rhoipites sp. 4

Plate 12, figures 1-2

Rhoipites sp. 4. Jardine and Harrington, 2008, p. 198, pl. 3, fig. 23.

Description. Monad pollen, radial, isopolar, prolate subprolate; tricolporate, colpi long, almost reach poles, lightly bordered by thickenings 0.5 – 1 μm wide, flare out at ora; ora large and lolongate, 3 – 6 x 6 – 10 μm wide, \pm unbordered; exine 1 – 2 μm thick, sexine:nexine ratio ~ 2:1; sexine columellate, semi-ectate, minutely microreticulate, lumina <0.5 μm wide, typically 0.2 – 0.3 μm wide, muri similar width to lumina.

Dimensions. Polar diameter 28 – 41 μm , mean 36 μm ; equatorial diameter 22 – 28 μm , mean 25 μm (eight specimens measured).

Remarks. *Rhoipites* sp. 4 differs from *Rhoipites* sp. 1 in having a much finer reticulum; otherwise the two taxa are very similar. *Rhoipites bradleyi* has a coarser reticulum than *Rhoipites* sp. 4, and lacks distinctly lolongate ora. *Rhoipites* sp. 5 is smaller and has endannulate ora.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 13/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert

Bluff Formation in Texas.

Rhoipites sp. 5

Plate 12, figures 3-4

Description. Monad pollen, radial, isopolar, subprolate; tricolporate, colpi almost reach the poles, bordered by thickenings 0.7 μm wide, widens to 1 μm wide at ora; ora lolongate, 6 x 2 μm , endannulate, endannuli 0.4 μm wide; exine 1.2 μm thick, sexine:nexine ratio 3:1; sexine distinctly columellate, semi-tectate, muri-clavate microreticulate, lumina and muri ~0.3 μm wide.

Dimensions. Polar diameter 24 μm ; equatorial diameter 18 μm (one specimen measured).

Remarks. This morphotype is differentiated from other reticulate tricolporate pollen by its very fine microreticulum and its lolongate ora. *Rhoipites* sp. 4 differs in being larger and in lacking endannuli.

Affinity. Unknown.

Occurrence. One specimen recorded in the Zilpha Formation on the eastern Gulf Coast.

Genus *Sandiegopollis* Frederiksen in Frederiksen et al. 1983

Type species. *Sandiegopollis elkeae* Frederiksen in Frederiksen et al. 1983.

Remarks. This genus accommodates heteropolar, reticulate tricolporate pollen,

whereby the lumina are coarser at one pole than at the other. The lumina often fine towards the mesocolpia, as with *Bombacacidites*. Also in common with *Bombacacidites*, and *Intratriporopollenites*, the grains are oblate, brevicolpate, and planaperturate. Both of these form genera differ from *Sandiegopollis* in being isopolar. *Friedrichipollis* Krutzsch 1970 differs from *Sandiegopollis* in being isopolar but being bireticulate, with a finely reticulate endosexine and a more coarsely reticulate ectosexine.

Sandiegopollis sp. 1

Plate 12, figures 5-7

Description. Monad pollen, radial, isopolar, \pm oblate, amb convex-triangular to subcircular; planaperturate, tricolporate, colpi short, reach under half way to poles, bordered by thickenings $\sim 2\ \mu\text{m}$ wide; ora vestibulate and endannulate, endannulus forms a semicircle, $2\ \mu\text{m}$ thick and $7 - 9\ \mu\text{m}$ wide; exine $1 - 1.5\ \mu\text{m}$ thick, sexine:nexine ratio 1:1-1.5; sexine microreticulate, reticulum heterobrochate and heteropolar, on one hemisphere lumina $0.5 - 1\ \mu\text{m}$ over the pole and $<0.5\ \mu\text{m}$ at the grain angles, on the other hemisphere lumina $0.3 - 0.5\ \mu\text{m}$ over the pole and $<0.2\ \mu\text{m}$ at the grain angles, except on one specimen where the finer hemisphere is homobrochate and has lumina $\sim 0.2\ \mu\text{m}$ in diameter over its entire surface. The lumina are typically polygonal but on the coarser hemisphere of one specimen the lumina within $\sim 5\ \mu\text{m}$ of the equator are elongated and aligned parallel to the equator. The muri are $<0.3\ \mu\text{m}$ wide and typically fine in concordance with the lumina.

Dimensions. Equatorial diameter $26 - 30\ \mu\text{m}$, mean $28\ \mu\text{m}$ (three specimens

measured).

Remarks. In overall appearance this taxon is most similar to *Intratriporopollenites instructus*, especially in terms of the vestibulate and heavily endannulate apertures. *Sandiegopollis* sp. 1 differs in being heteropolar and smaller. The two *Sandiegopollis* taxa illustrated in Frederiksen (in Frederiksen et al., 1983) differ in being more coarsely reticulate on both hemispheres, and in having apertures that are more similar to *Bombacacidites* than *Intratriporopollenites*.

Affinity. Frederiksen (in Frederiksen et al., 1983) suggested Sterculioideae or Tilioideae of the Malvaceae *s.l.* as possible parent plant families for pollen of this type, as both contain species that produce pollen with heteropolar reticula. Given the tiloid nature of the apertures in *Sandiegopollis* sp. 1, Tilioideae is perhaps most likely.

Occurrence. Three specimens recorded in the Hatchetigbee Formation on the eastern US Gulf Coast.

Genus *Symplocos* Jacquin

Remarks. Pollen of extant *Symplocos* is peroblate, brevicolpate and vestibulate. It encompasses many of the morphotypes that have been assigned to either *Porocolpopollenites* or *Symplocoipollenites* (Frederiksen, 1980a). While the assignment of fossil pollen of this morphological type to the family Symplocaceae is uncontroversial, Frederiksen (1988) chose to express uncertainty in assigning species to the modern genus by using the name '*Symplocos?*' Here, I have followed the same practice.

Symplocos? sp. 1

Plate 13, figures 3-4

Description. Monad pollen, radial, isopolar, \pm oblate, amb obtuse-concave-triangular with broad angles; tricolporate, colpi short, reach under half way to poles, 3 μm wide at equator, unbordered; ora vestibulate, vestibula 5 μm wide and 1 μm deep, endannulate, endannuli extend \sim 5 μm either side of ora; exine in inter-apertural areas \sim 1 μm thick, sexine thins towards apertures but shows a slight tumescence over the vestibulum; nexine indistinct, sexine punctate, punctae \sim 0.2 μm in diameter.

Dimensions. Equatorial diameter 25 μm (one specimen measured).

Remarks. *Symplocos? contracta* has a punctate exine but differs in having a straight to convex sided amb and a slit-like vestibulum, and in lacking endannuli. *Symplocos? jacksoniana* Traverse 1955 is more distinctly concave and has narrower angles.

Symplocos? sp. 2 is larger and is less distinctly punctate.

Affinity. Probably *Symplocos* (Symplocaceae).

Occurrence. Four specimens recorded in the Calvert Bluff Formation in Texas.

Symplocos? sp. 2

Plate 13, figure 5

Description. Monad pollen, radial, isopolar, \pm oblate, amb obtuse-concave-triangular; tricolporate, colpi short, reach \sim 1/3 of way to poles, 4 μm wide at equator, unbordered; ora vestibulate, vestibula 10 μm wide and 1 μm deep; exine 1.5 μm

thick, sexine:nexine ratio 1:1.5; sexine indistinctly columellate, punctate, punctae ~0.1 µm in diameter.

Dimensions. Equatorial diameter 40 µm (one specimen measured).

Remarks. This specimen is distinguished from other *Syplocos?* types by its large size and indistinct ornamentation. “cf. *Symplocoipollenites* sp.” Elsik 1968 is a similar size to *Syplocos?* sp. 2, but differs in having a convex-triangular to subcircular amb, a more complicated aperture structure, and nexinal striations.

Affinity. Probably *Syplocos* (Symplocaceae).

Occurrence. Two specimens recorded in the Tuscaloosa Formation on the eastern US Gulf Coast.

Genus *Tricolporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type species. *Tricolporopollenites dolium* (Potonié 1931) Thomson & Pflug 1953.

Remarks. The diagnosis of this genus, as formulated by Pflug and Thomson (in Thomson and Pflug, 1953), includes almost all tricolporate pollen. As with *Tricolporopollenites* for tricolporate taxa, *Tricolporopollenites* is useful for accommodating tricolporate morphotypes that do not fit comfortably into other existing form genera.

Tricolporopollenites sp. 1

Plate 13, figure 10

Description. Monad pollen, radial, isopolar, prolate spheroidal; tricolporate, colpi

almost reach the poles, $\sim 1\text{ }\mu\text{m}$ wide, bordered by thickenings $0.6\text{ }\mu\text{m}$ wide; ora lolongate, $5 \times 2\text{ }\mu\text{m}$ in diameter, bordered by thickenings $0.6\text{ }\mu\text{m}$ wide; exine $\sim 1\text{ }\mu\text{m}$ thick, sexine:nexine ratio 1:1.5; sexine columellate and punctate, punctae $\sim 0.2\text{ }\mu\text{m}$ in diameter.

Dimensions. Polar diameter $26\text{ }\mu\text{m}$; equatorial diameter $20\text{ }\mu\text{m}$ (one specimen measured).

Remarks. Although this specimen is tricolporate and punctate, its distinctly lolongate ora mean that it does not fit within the circumscription of *Nyssapollenites*.

Affinity. Unknown.

Occurrence. One specimen recorded in the Tuscaloosa Formation on the eastern US Gulf Coast.

Tricolporopollenites sp. 2

Plate 13, figure 11

Description. Monad pollen, radial, isopolar, prolate spheroidal; tricolporate, colpi almost reach the poles, $\sim 1\text{ }\mu\text{m}$ wide, lightly bordered by thickened margins, costae colpi well-developed and $\sim 0.5\text{ }\mu\text{m}$ wide, width increases to $1\text{ }\mu\text{m}$ at ora; endopore lolongate, $5 \times 3\text{ }\mu\text{m}$ in diameter, unbordered; exine $\sim 1\text{ }\mu\text{m}$ thick, sexine:nexine ratio 2:1; sexine evenly granulate.

Dimensions. Polar diameter $30\text{ }\mu\text{m}$; equatorial diameter $26\text{ }\mu\text{m}$ (one specimen measured).

Remarks. This specimen has lolongate ora, a granulate exine and is almost

spheroidal in shape. *Tricolporopollenites* sp. 4 is also \pm spheroidal but is much smaller and has a distinctly punctate exine.

Affinity. Unknown.

Occurrence. One specimen recorded in the Naheola Formation on the eastern US Gulf Coast.

Tricolporopollenites sp. 3

Plate 13, figure 12

Tricolporopollenites sp. 3. Jardine and Harrington, 2008, p. 198, pl. 4, fig. 1.

Description. Monad pollen, radial, isopolar, amb obtuse-convex-triangular; tricolporate, colpi extend 3/4 of way to pole, in polar view the upper (polewards) half of the colpi are thin and slit-like, but gape open towards the equator, at the equator the colpi are about 6 μm wide, costae colpi 1-2 μm thick, margins hardly thickened if at all; ora endannulate, endannuli \sim 2 μm thick and 8 μm wide, positioned just in front of where the colpi begin to open out, the ora are presumably large and cause the colpi to gape open around them; exine 1 μm thick, sexine:nexine ratio 1:1; sexine columellate, tectate, punctate to microreticulate, lumina and muri \sim 0.3 μm wide.

Dimensions. Equatorial diameter 45 μm (one specimen measured).

Remarks. This specimen is distinguished by its long colpi that gape open about the equator. *Holkopollenites* has more deeply incised colpi and nexinal striations, and cf. *Symplocoipollenites* has vestibulate ora, shorter colpi and also possesses nexinal

striations.

Affinity. Unknown.

Occurrence. One specimen recorded at the base of the Tuscahoma Formation on the eastern US Gulf Coast.

Tricolporopollenites sp. 4

Plate 13, figures 13-14

Description. Monad pollen, radial, isopolar, spheroidal; tricolporate, brevicolpate, colpi extend ~1/2 way to the poles, slit-like, unbordered and indistinct; ectopore poorly developed, endopore large, circular to lalongate, 5 μm wide, bordered above and below by endannuli that extend 3 μm polewards of ora; exine 1.2 μm thick, sexine:nexine ratio 1:2.5; sexine microreticulate, lumina ~0.3 μm wide, muri slightly less than this.

Dimensions. Polar diameter 17 μm ; equatorial diameter 16 μm (one specimen measured).

Remarks. This specimen is small and spheroidal, and has large, circular, endannulate ora, a thick nexine and a microreticulate sexine. The *Siltaria-Cyrrillaceaepollenites* complex accommodates spheroidal psilate to scabrate grains with more or less geniculate colpi and lalongate, elliptical ora.

Affinity. Unknown.

Occurrence. One specimen recorded in the Naheola Formation on the eastern Gulf Coast.

ZONOCOLPORATE POLLEN

Genus *Bombacacidites* Couper 1960

Type species. *Bombacacidites bombaxoides* Couper 1960.

Remarks. *Bombacacidites* pollen is peroblate to oblate, brevicolporate, plan-aperturate, and has a reticulate or retipilate sculpture in which the lumina are larger on the apocolpia and fine towards the mesocolpia and colpi. Individual species are defined based on the diameter of the lumina across the grain, and on their amb shape, which is usually triangular but may be circular. *Intratropipollenites* differs in being infrareticulate rather than supracreticulate, in having lumina of a uniform size across the grain, and in having vestibulate pores with well-developed endannuli.

?*Bombacacidites* sp. 1

Plate 13, figure 18

Description. Monad pollen, radial, isopolar, amb subcircular, grain \pm oblate; pentacolporate, colpi short and horse-shoe shaped, extend 1/3 of the way to the poles, bordered by thickenings 1 μ m wide; ora distinctly endannulate, endannuli 2 μ m thick and extending 2-3 μ m either side of ora, ora not vestibulate; exine 1.2 μ m thick, sexine:nexine ratio 2.5:1; sexine columellate, semi-tectate, muri-clavate reticulate, heterobrochate but no decrease in size of lumina from apocolpia to mesocolpia, lumina 1-3 μ m wide, irregular to elongated angular in shape, muri \sim 0.25 μ m wide,

simplibaculate.

Dimensions. Equatorial diameter 46 μm (one specimen measured).

Remarks. This specimen shows no decrease in lumina size from the apocolpia to the mesocolpia, and so the assignment to *Bombacacidites* is only tentative. However, the grain does possess morphological features that are diagnostic of *Bombacacidites*, such as being oblate, planaperturate and reticulate, and having ora that are not vestibulate, and short colpi that have thickened margins.

Affinity. Possibly Bombacoideae of the Malvaceae *s.l.* Pollen of this subfamily is usually tri-aperturate, but much variation does exist in the extant species (Erdtman, 1952).

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Pentacolporate pollen sp. 1

Plate 13, figure 19

Description. Monad pollen, radial, isopolar, amb circular, grain \pm oblate; pentacolporate, colpi extend 1/4 of the way to the poles, unbordered; ora endannulate, endannuli 1 μm thick and extending \sim 1.5 μm either side of ora, some evidence for arci joining ora, but this may be folding of the grain following dispersal; exine 0.8 μm thick, sexine:nexine ratio 1:2 excluding surface sculpture; surface of grain sparsely and irregularly covered in echinae <1 μm long.

Dimensions. Equatorial diameter 42 μm (one specimen measured).

Remarks. The ora on this grain are indistinct and are only evidenced by the presence of endannuli. Pentacolpate pollen sp. 1 differs in lacking echinae and ora.

Affinity. Unknown. This specimen is superficially similar to pollen of *Nothofagus* Blume and *Nothofagacidites* Potonié 1960, in that it is polyaperturate, brevicolpate, oblate, and is ornamented with microechinae. However, pollen of *Nothofagus* lacks ora, and has well-thickened colpi margins.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Genus *Porocolpopollenites* Pflug in Thomson & Pflug 1953

Porocolpopollenites sp. 4

Plate 13, figure 20

Description. Monad pollen, radial, isopolar, amb ±circular, grain ±oblate; pentacolporate, colpi extend ~1/2 of the way to the poles, 2 µm wide at equator, margins not thickened but costae colpi 2 µm wide present, straight sided at rounded at the ends of the colpi, bordered by zone of thinned nexine ~1 µm wide; ora endannulate, endannuli 1 µm thick and 6 µm wide, vestibulae narrow in polar view, <0.5 µm wide; exine 1 µm thick, sexine:nexine ratio 3:1; sexine atectate, surface smooth to finely scabrate.

Dimensions. Equatorial diameter 32 µm (one specimen measured).

Remarks. This specimen is characterised by the wide, well-rounded nexinal

thickenings bordering the colpi, the very narrow vestibulae, and by being pentacolporate. *Porocolpopollenites* sp. 2 is tri-aperturate, and has longer colpi are bordered by thickenings with more pointed ends. *Porocolpopollenites ollivierae* is tri- to tetra-aperturate and has boat-shaped colpi that are bordered by sexinal thickenings.

Affinity. Unknown.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Genus *Retistephanocolporites* Van der Hammen & Wijmstra 1964

Type species. *Retistephanocolporites quadriporus* Van der Hammen & Wijmstra 1964.

Remarks. *Retistephanocolporites* includes zonocolporate pollen grains with a reticulate sculpture. The type species of the genus is extremely brevicolpate, but this is not a diagnostic feature of the genus as a whole. *Caprifoliipites*, *Horniella* and *Rhoipites* are reticulate but exclusively tricolporate.

Retistephanocolporites sp. 1

Plate 13, figures 25-26

Description. Monad pollen, radial, isopolar, subprolate; tetracolporate, colpi almost reach the poles, bordered by thickenings 1 µm wide; ora slightly lalongate, 3 x 2 µm, weakly endannulate, endannuli ~1 µm wide above and below ora; exine 1 µm thick, sexine:nexine ratio 2:1; sexine columellate, semi-tectate, reticulate, heterobrochate,

lumina 0.5 – 1.5 μm wide, irregular in shape, muri ~ 0.3 μm wide.

Dimensions. Polar diameter 29 μm , equatorial diameter 21 μm (one specimen measured).

Remarks. If this grain were tricolporate it would fit comfortably into *Horniella*, because it possesses only weakly bordered colpi and lalongate ora. Other tetracolporate pollen in this dataset is either oblate, or lacks a reticulate sculpture.

Affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

TRIPROJECTATE POLLEN

Genus *Aquilapollenites* Rouse 1957 emend. Funkhouser 1961

Type species. *Aquilapollenites quadrilobus* Rouse 1957.

Remarks. *Aquilapollenites* is characterised by the presence of three equatorial protrusions, and one or more polar protrusions (i.e. one or both of the poles is/are extended to project out from the grain). *Aquilapollenites* pollen can therefore be either isopolar or heteropolar. The apertures typically comprise three colpi or three pairs of demicolpi situated on the equatorial protrusions. There may additionally be three colpi on and/or parallel to the equator between the equatorial protrusions. The sculpture is variable between species. This genus is typical of Cretaceous sediments (Traverse, 1988; Srivastava, 1994), and the specimens described here may

be reworked.

Aquilapollenites sp. 1

Plate 14, figure 5

Description. Isopolar; poles pulled out into prominent protrusions that widen from ~9 µm at their tips to ~16 µm where they meet the main body of the grain; three wing-like equatorial protrusions ~6 µm in diameter; tridemicolpate, demicolpi begin 1/2 way along the equatorial protrusions and extend to 1/2 way along the protruded poles, bordered by thickenings that are 3 µm wide in the middle of the demicolpi and thin towards the ends of the demicolpi; exine ~1 µm thick, smooth on equatorial protrusions and microreticulate on polar protrusions, reticulum heterobrochate, lumina 0.1 – 0.6 µm in diameter, fine towards tips of polar protrusions, muri ~0.2 µm wide.

Dimensions. Polar diameter 35 µm; tip of equatorial protrusions to polar axis 15 µm.

Remarks. This taxon is characterised by its heavily thickened colpi and microreticulate exine on the polar protrusions. *Aquilapollenites attenuatus* also has thickened colpi and is isopolar, but has a punctate and echinate exine.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Aquilapollenites sp. 2

Plate 14, figure 6

Description. Isopolar; poles pulled out into prominent protrusions ~12 μm in diameter; three wing-like equatorial protrusions ~8 μm in diameter; tridemicolpate, demicolpi begin 2/3 of the way along the equatorial protrusions and extend to 2/3 of the way along the protruded poles, bordered by thickenings that are 2 μm wide in the middle of the demicolpi and thin towards the ends of the demicolpi; exine ~1.5 μm thick, ornamentation the Bertillon pattern of Funkhouser (1961) (= raised lines resembling a fingerprint), exine underneath this punctate.

Dimensions. Polar diameter 30 μm ; tip of equatorial protrusions to polar axis 18 μm .

Remarks. *Aquilapollenites bertillonites* Funkhouser 1961 has a similar ornamentation, but has attenuated equatorial protrusions with bulges located between them, and is tricolpate with the colpi located at the tips of the equatorial protrusions.

Affinity. Unknown.

Occurrence. One specimen recorded in the Calvert Bluff Formation in Texas.

Aquilapollenites sp. 3

Plate 14, figure 7

Description. Heteropolar; one pole extended into a slight protrusion 12 μm in diameter; the other concave with respect to the three equatorial protrusions; equatorial protrusions ~8 μm in diameter; tridemicolpate, colpi extend about 1/2

way up protruded pole, colpi on reduced pole may meet to be syncolpate; exine ~1 μm thick, reticulate, heterobrochate, fines from <1 μm on main body to ~0.2 μm on protrusion ends, row of inward pointing bacula present along equatorial protrusions.

Dimensions. Polar diameter ~20 μm ; tip of equatorial protrusions to polar axis ~17 μm (grain at oblique angle so measurements approximate).

Remarks. *Aquilapollenites* sp. 4 is larger, has a reticulate polar protrusion and punctate equatorial protrusions, and has a row of inward pointing echinae lining the equatorial protrusions, rather than bacula.

Affinity. Unknown.

Occurrence. One specimen recorded in the Porters Creek Formation on the eastern Gulf Coast.

Aquilapollenites sp. 4

Plate 14, figure 8

Description. Heteropolar; one pole extended into a prominent protrusion 12 μm in diameter; the other pole not observed in this grain; equatorial protrusions 13 μm in diameter; colpi unbordered and obscure; exine ~1 μm thick, polar protrusion coarsely reticulate and echinate, lumina 1 – 2 μm wide, muri 0.75 μm wide, echinae ~2 μm long; equatorial protrusions punctate and evenly echinate, echinae spaced 2 – 5 μm apart, edges of equatorial protrusions lined with an inward pointing row of echinae, individual echinae on edge of protrusions are triangular and ~1 μm high ~1 μm wide at the base.

Dimensions. Polar diameter ~30 μm ; tip of equatorial protrusions to polar axis ~30 μm (grain at oblique angle so measurements approximate).

Remarks. *Aquilapollenites* sp. 3 is smaller, has a microreticulate exine, and has a row of inward pointing baculae lining the equatorial protrusions, rather than echinae.

Affinity. Unknown.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Aquilapollenites sp. 5

Plate 14, figure 9

Description. Isopolar; poles pulled out into prominent protrusions 12 μm in diameter; three wing-like equatorial protrusions ~ 10 μm in diameter; colpi unbordered and obscure, tridemicolpate?; exine <1 μm thick, polar projections retistriate, lumina ~0.5 μm wide, muri ~0.25 μm wide, equatorial projections punctate and finely striate, with striae aligned parallel to the polar axis.

Dimensions. Polar diameter 48 μm ; tip of equatorial protrusions to polar axis 20 μm .

Remarks. *Aquilapollenites striatus* Funkhouser 1961 has a striate exine but is heteropolar rather than isopolar. *Aquilapollenites* sp. 1 and sp. 2 are isopolar but are not striate or retistriate.

Affinity. Unknown.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Aquilapollenites sp. 6

Plate 14, figures 10-11

Description. Heteropolar; one pole pulled out into a prominent protrusion 9 μm in diameter; the other pole concave with respect to the three equatorial protrusions; equatorial protrusions $\sim 10\ \mu\text{m}$ wide; colpi unbordered and obscure, tridemicolpate?; exine $\sim 0.5\ \mu\text{m}$ thick and indistinctly columellate over most of grain, thickens to $1\ \mu\text{m}$ thick and becomes distinctly columellate towards end of polar protrusion; exine punctate – minutely microreticulate over most of grain, lumina and muri $\sim 0.2\ \mu\text{m}$ wide, band $\sim 8\ \mu\text{m}$ wide on lower half of polar protrusion is more coarsely reticulate, with lumina $0.5 - 1\ \mu\text{m}$ wide and muri $\sim 0.2\ \mu\text{m}$ wide, contact between this band and surrounding exine gradational, patch of similar exine on lower (unprotruded) pole, supratectal echinae $\sim 1\ \mu\text{m}$ long are sparsely distributed over whole grain.

Dimensions. Polar diameter $35\ \mu\text{m}$; tip of equatorial protrusions to polar axis $36\ \mu\text{m}$.

Remarks. This taxon is differentiated from other *Aquilapollenites* types by the band of reticulate exine on the polar protrusion. *Aquilapollenites pulcher* Funkhouser 1961 and *Aquilapollenites polaris* Funkhouser 1961 are both heteropolar and have punctate and echinate sculptures, but they lack the areas of reticulate exine, and they have shorter and thicker protrusions. *Aquilapollenites pulcher* is only punctate on the same parts of the grain as *Aquilapollenites* sp. 6 is reticulate.

Affinity. Unknown.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast.

Aquilapollenites sp. 7

Plate 14, figures 12-13

Description. Heteropolar; one pole pulled out into a prominent protrusion 10 μm in diameter; the other pole pulled out into a slight protrusion ~ 4 μm long; equatorial protrusions 25 μm wide where they meet the main body of the grain, 10 μm wide at near ends, ends rounded in equatorial view; tridemicolpate, upper demicolpi ~ 15 μm long, lower demicolpi ~ 8 μm long, positioned centrally along length of equatorial protrusions, bordered by thickenings 1 μm wide at the centre and narrowing towards the colpi ends; exine ~ 1 μm thick, columellate, minutely punctate and evenly covered with small echinae < 1 μm long.

Dimensions. Polar diameter 30 μm ; tip of equatorial protrusions to polar axis 20 μm .

Remarks. *Aquilapollenites polaris* Funkhouser 1961 is superficially very similar to this specimen, but on that taxon the echinae on the equatorial protrusions are confined to a median band which expands towards the ends of the protrusions. *Aquilapollenites pulcher* Funkhouser 1961 has is only punctate on the short polar protrusion and at the base of the long polar protrusion.

Affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

PLATES

All photomicrographs were taken at x1000 magnification and under phase contrast, unless otherwise indicated. The taxon name is followed by the formation and state that the sample was taken from, the sample name, and the England Finder (EF) coordinate for the photographed specimen.

PLATE 1

- 1 *Laevigatosporites haardtii*; Tuscahoma Formation, Alabama, GH08/Wa/027, EF Q33/1.
- 2 *Microfoveolatosporis pseudodentatus*; Hatchetigbee Formation, Mississippi, GH00/Ht/013A, EF N19/4.
- 3 *Polypodiisporonites* spp.; Calvert Bluff Formation, Texas, UCB/08/007, EF L33/centre.
- 4 *Reticuloidosporites* spp.; Naheola Formation, Alabama, TUC/08/023, EF E28/centre.
- 5 *Appendicisporites* spp.; Porters Creek Formation, Alabama, TUC/08/031, EF T28/centre.
- 6-7 *Baculatisporites primarius*; same specimen at different focal levels, Hatchetigbee Formation, Alabama, WAH/08/075, EF T23/3.
- 8-9 *Bullasporis* spp.; same specimen at different focal levels, Nanafalia Formation, Alabama, GH08/Wa/006, EF L34/centre.
- 10-11 *Camarazonosporites grootii*; same specimen at different focal levels, Nanafalia Formation, Alabama, GH08/Wa/005, EF H34/3.
- 12 *Camarazonosporites heskamensis*; Hatchetigbee Formation, Mississippi, GH00/Ht/26, EF S38/2.
- 13 *Camarazonosporites* sp. 1; Nanafalia Formation, Mississippi, GH00/AC/004, EF M40/1.
- 14 *Cicatricosisporites dorogensis*; Hatchetigbee Formation, Mississippi, GH00/Ht/057A, EF W37/2.
- 15 *Deltoidospora* spp.; Nanafalia Formation, Mississippi, GH00/AC/002, EF E31/centre.

PLATE 1



1



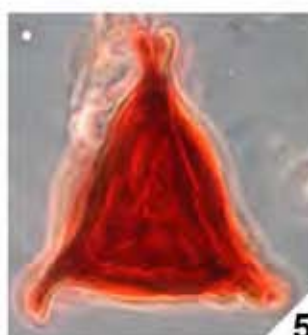
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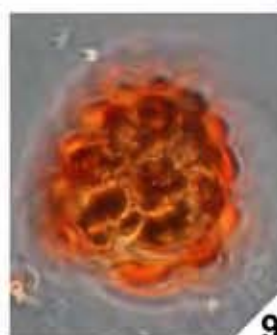
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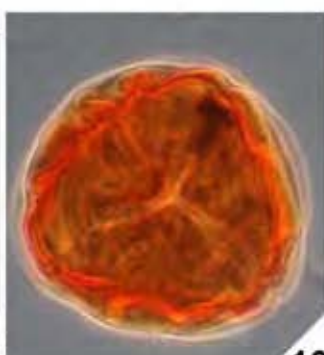
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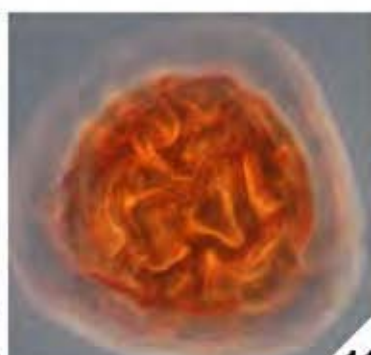
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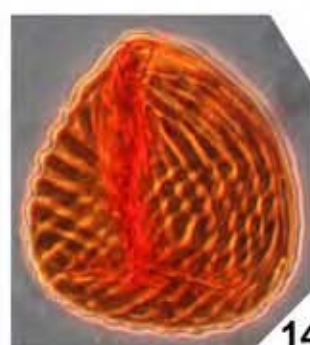
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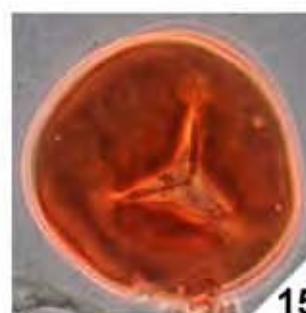
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14



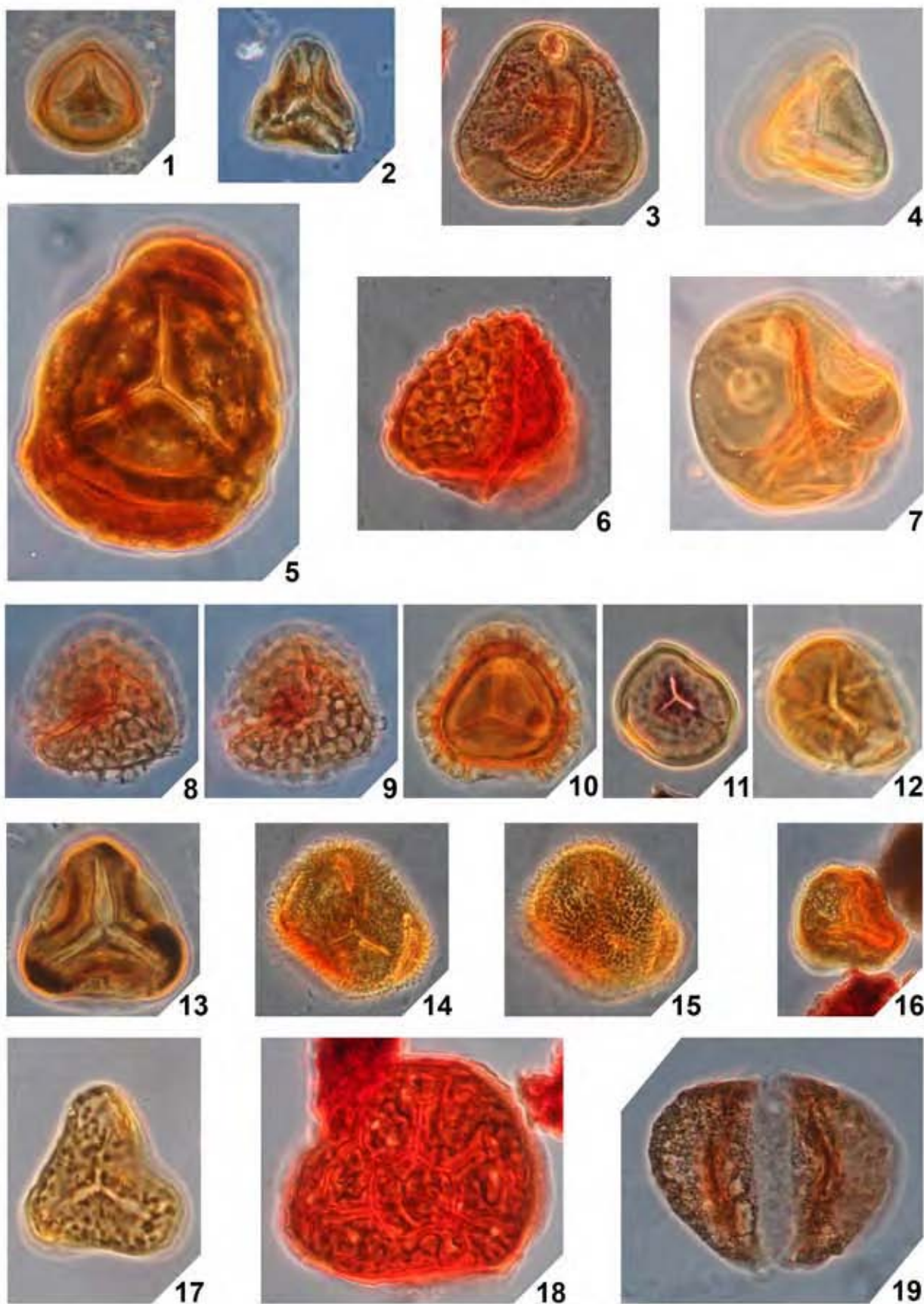
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10 μ m

PLATE 2

- 1 *Cingulatisporites* spp.; Naheola Formation, Alabama, TUC/08/020, EF N37/2.
- 2 *Gleicheniidites senonicus*; Hatchetigbee Formation, Alabama, WAH/08/074, EF E38/1.
- 3 *Granulatisporites luteticus*; Hatchetigbee Formation, Mississippi, GH00/Ht/013A, EF W37/1.
- 4 *Leiotriletes* spp.; Calvert Bluff Formation, Texas, BGC/08/001, EF P28/2.
- 5 *Patellasperites* spp.; Naheola Formation, Alabama, TUC/08/023, EF M27/2.
- 6 *Microreticulatisporites* spp.; Nanafalia Formation, Mississippi, GH00/AC/002, EF Y36/2.
- 7 *Punctatisporites* spp.; Calvert Bluff Formation, Texas, UCB/08/005, EF X22/centre.
- 8-10 *Retitriletes* spp.; 8-9, distal face, same specimen at different focal levels, Hatchetigbee Formation, Alabama, WAH/08/072, EF E33/1; 10, proximal face, Naheola Formation, Alabama, TUC/08/020, EF S41/1.
- 11 *Stereisporites granistereooides*; Tuscahoma Formation, Mississippi, GH00/AC/009, EF T36/3.
- 12 *Stereisporites stereooides*; Calvert Bluff Formation, Texas, WCM/08/024, EF O23/4.
- 13 *Toroisporis* spp.; Naheola Formation, Alabama, TUC/08/020, EF O37/3.
- 14-15 Trilete spore, clavate; same specimen at different focal levels, Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF V41/2.
- 16 Trilete spore, reticulate; Hatchetigbee Formation, Mississippi, GH00/Ht/001A, EF S35/1.
- 17 Trilete spore, verrucate; Calvert Bluff Formation, Texas, WCM/08/020, EF X25/1.
- 18 *Zlivisporis novamexicanum*; Hatchetigbee Formation, Mississippi, GH00/Ht/026, X24/centre.
- 19 Bisaccate pollen; Porters Creek Formation, Alabama, TUC/08/016, EF H25/4.

PLATE 2



10 μm

PLATE 3

- 1-4 Bisaccate pollen; 1-3, Hatchetigbee Formation, Alabama; 1, WAH/08/075, EF Q29/2; 2, WAH/08/072, EF R36/3; 3, WAH/08/077, EF T22/centre; 4, Tuscahoma Formation, Mississippi, GH00/AC/11A, EF K15/1.
- 5 *Cupressacites hiatipites*; Tuscahoma Formation, Alabama, GH08/Wa/048, EF V38/centre.
- 6 *Ephedripites* subgenus *Spiralipites* spp.; Calvert Bluff Formation, Texas, UCB/08/005, EF Y34/1.
- 7 *Sequoiapollenites* spp.; Naheola Formation, Alabama, TUC/08/020, EF V38/centre.
- 8-9 *Milfordia hungarica*; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH00/Ha/088, EF V27/2.
- 10 *Milfordia minima*; Hatchetigbee Formation, Mississippi, GH00/Ht/057A, EF W27/4.
- 11 *Sparganiaceapollenites* spp.; Hatchetigbee Formation, Mississippi, GH00/Ht/001A, EF U17/1.
- 12 *Basopollis obscurocostatus*; Tallahatta Formation, Mississippi, GH00/Ha/085, EF Q38/1.
- 13-14 Betulaceae/Myricaceae type; 13, Nanafalia Formation, Mississippi, GH08/KC/026, EF M35/centre; 14, Tuscahoma Formation, Mississippi, GH00/AC/009, EF X25/4.
- 15-16 *Brosipollis striata*; Hatchetigbee Formation, Mississippi; 15, GH00/Ht/071A, EF T41/centre; 16, GH00/Ht/047, EF T26/4.
- 17 *Caryapollenites imparalis* group; Hatchetigbee Formation, Mississippi; GH00/Ht/36, EF Q35/centre.
- 18 *Caryapollenites veripites*; Tuscahoma Formation, Mississippi, GH08/Wa/027, EF R40/4.
- 19 *Caryapollenites wodehousei*; Hatchetigbee Formation, Mississippi, GH00/Ht/036, EF T38/4.
- 20 *Choanopollenites alabamicus*; Calvert Bluff Formation, Texas, WCM/08/027, EF U27/3.

PLATE 3

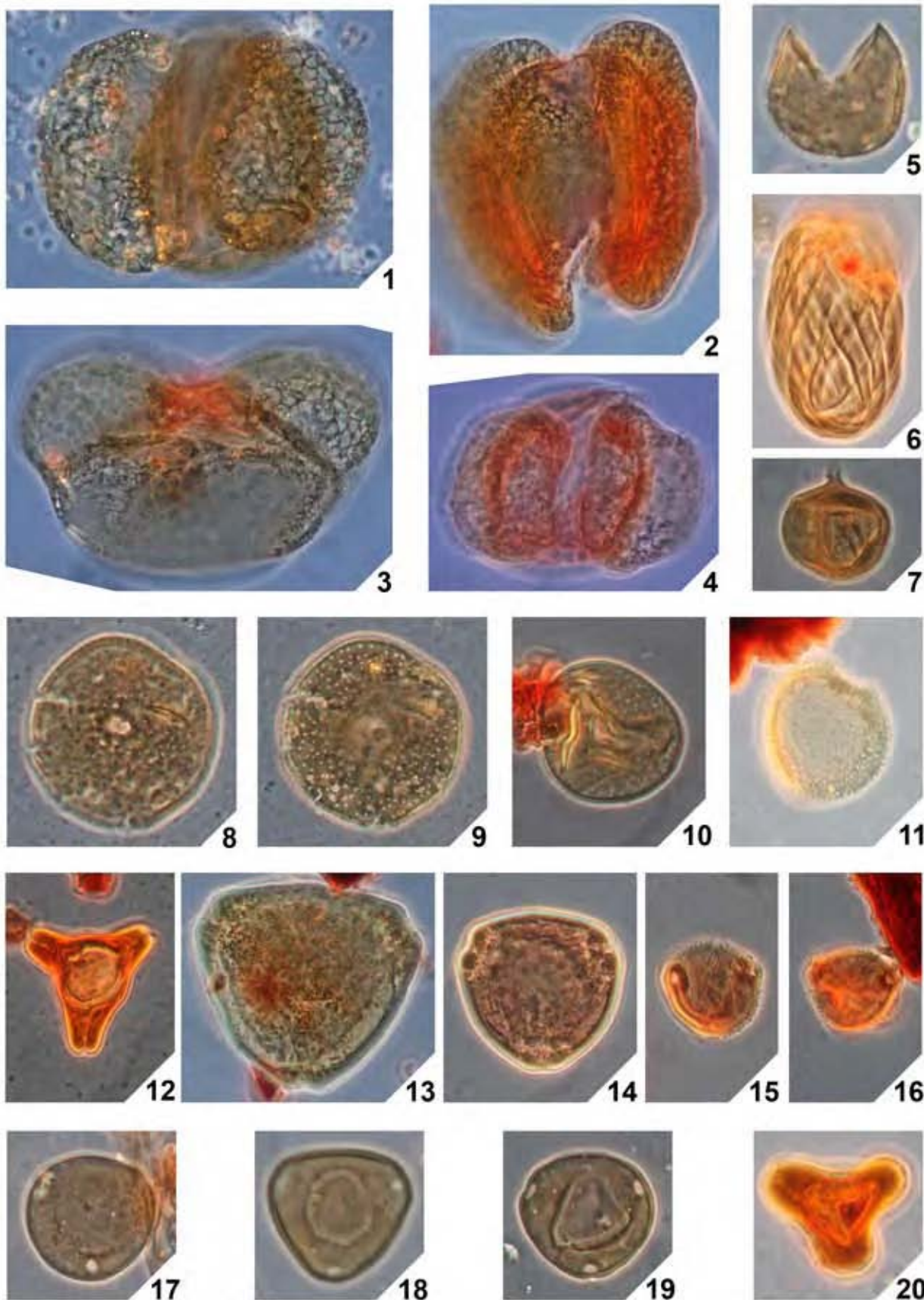
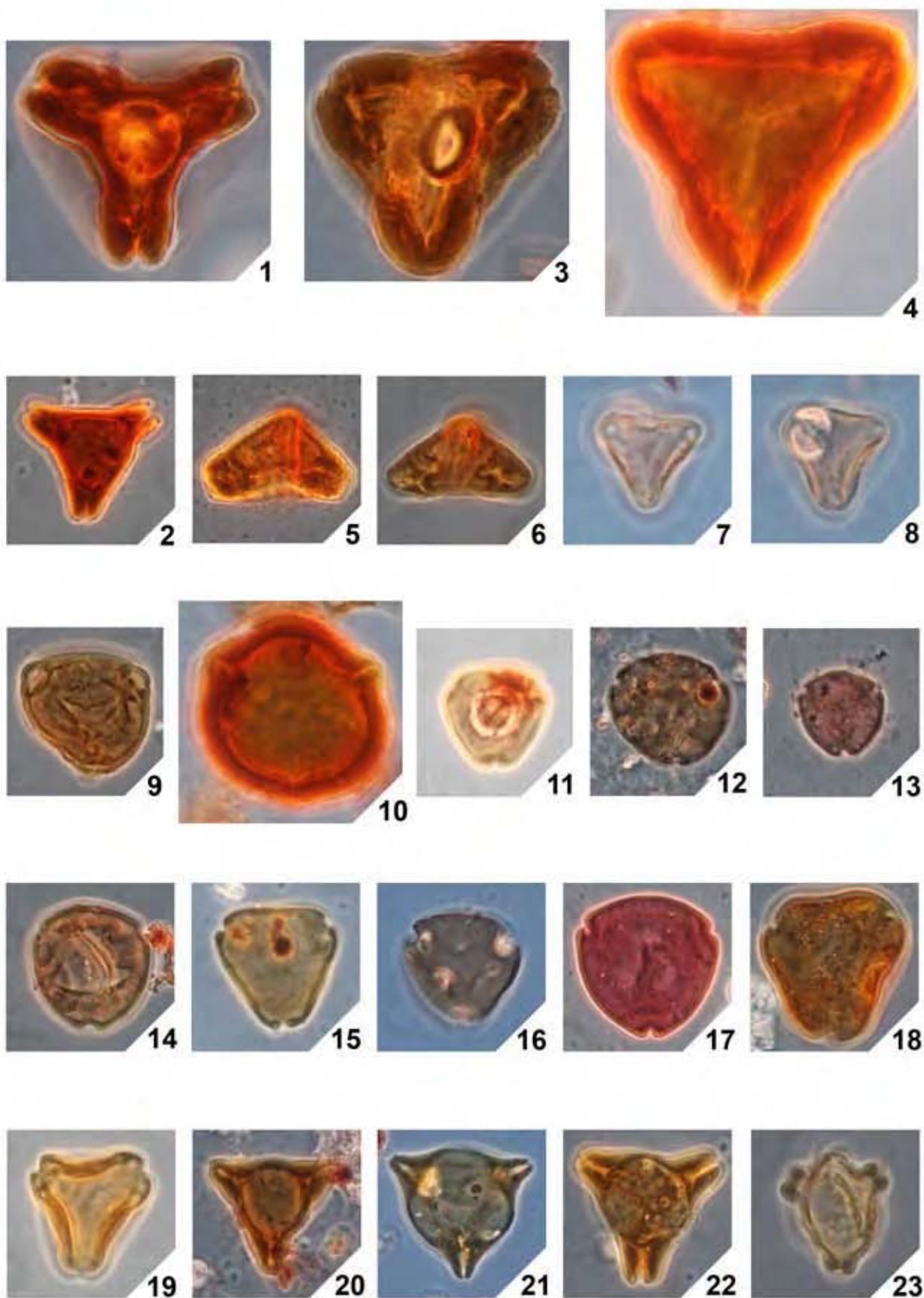


PLATE 4

- 1 *Choanopollenites conspicuus*; Naheola Formation, Alabama, GH08/Wa/004, EF O35/4.
- 2 *Choanopollenites discipulus*; Porters Creek Formation, Alabama, TUC/08/008, EF J40/centre.
- 3 *Choanopollenites patricius*; Nanafalia Formation, Mississippi, GH08/KC/022, EF U38/2.
- 4 *Choanopollenites* sp. cf. *Choanopollenites eximius*; Calvert Bluff Formation, Texas, WCM/08/031, EF J31/2.
- 5-6 *Complexiopollis* spp.; 5, Tallahatta Formation, Mississippi, GH00/Ha/085, EF L36/3; 6, Nanafalia Formation, Mississippi, GH08/KC/006, EF V29/4.
- 7-8 *Interpollis microsupplingensis*; same specimen at different focal levels, Hatchetigbee Formation, WAH/08/066, EF G17/3.
- 9 *Interpollis paleocenica*; Naheola Formation, Mississippi, JDC/08/037, EF P29/centre.
- 10 *Kyandopollenites anneratus*; Tuscahoma Formation, Alabama, GH08/Wa/051, EF Q33/1.
- 11 *Momipites anellus*; Hatchetigbee Formation, Mississippi, GH00/Ht/001A, EF S25/1.
- 12 *Momipites coryloides*; Naheola Formation, Mississippi, JDC/08/043, EF V25/1.
- 13 *Momipites microfoveolatus*; Tuscahoma Formation, Mississippi, GH00/AC/013, EF Q28/3.
- 14 *Momipites nicholsii*; Tallahatta Formation, Mississippi, GH00/Ha/089, EF J30/1.
- 15 *Momipites strictus*; Tuscahoma Formation, Mississippi, GH08/Wa/048, EF D25/2.
- 16 *Momipites triradiatus* type; Hatchetigbee Formation, Alabama, WAH/08/072, EF X32/centre.
- 17 *Momipites ventifluminis*; Tuscahoma Formation, Mississippi, GH00/AC/013, EF V17/3.
- 18 *Momipites waltmanensis*; Naheola Formation, Alabama, TUC/08/020, EF V29/1.
- 19 "*Momipites* cf. *M. flexus*" of Frederiksen 1998; Calvert Bluff Formation, Texas, UCB/08/008, EF W30/1.
- 20 *Nudopollis endangulatus*; Naheola Formation, Mississippi, JDC/08/043, EF S23/4.
- 21 *Nudopollis terminalis*; Hatchetigbee Formation, Alabama, WAH/08/077, EF T27/2.
- 22 *Nudopollis thiergartii*; Nanafalia Formation, Alabama, WAH/08/011, EF S35/centre.
- 23 *Paraalnipollenites confusus*; Nanafalia Formation, Mississippi, GH08/KC/022, EF P43/1.

PLATE 4

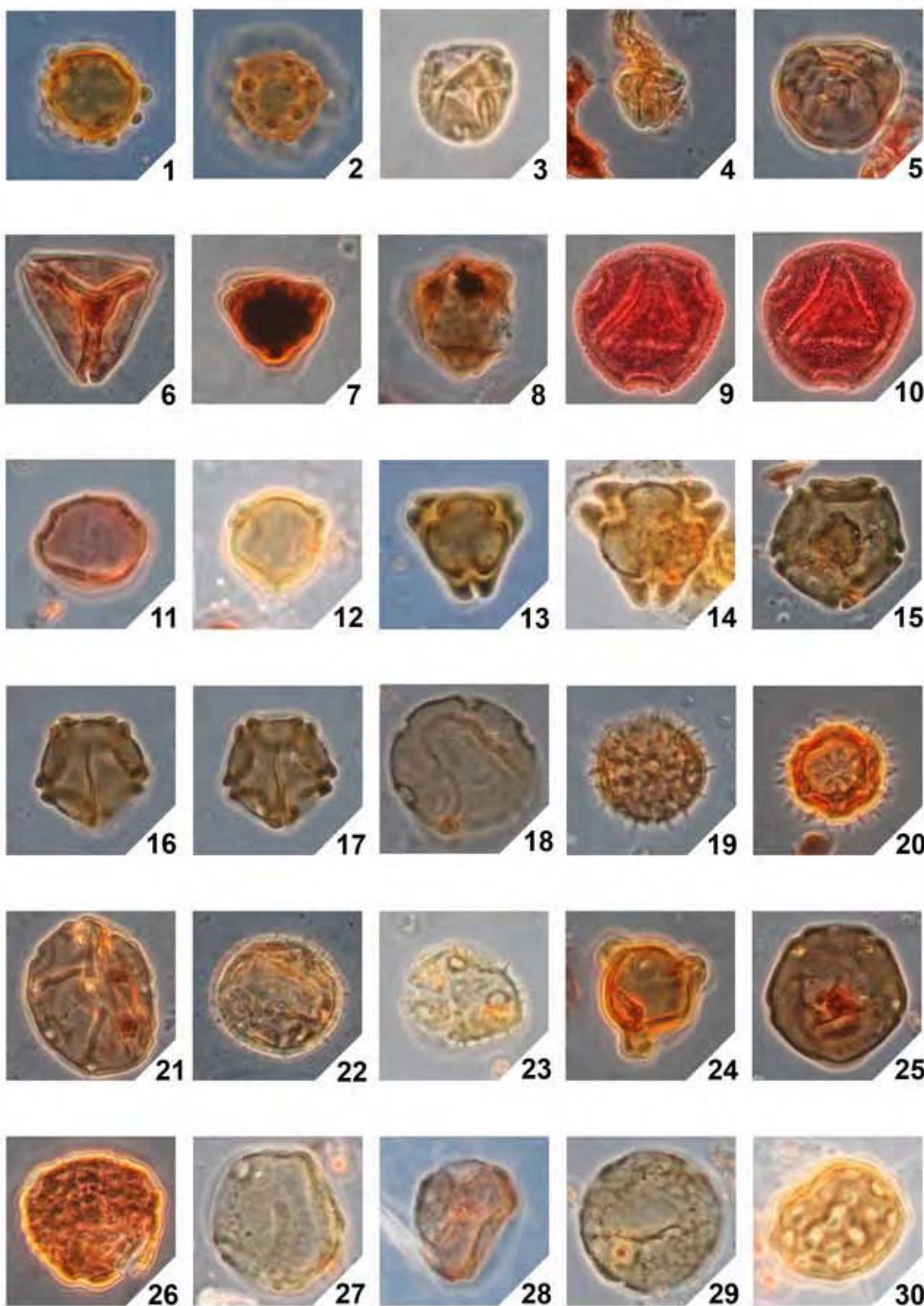


10 μm

PLATE 5

- 1-2 *Pistillipollenites mcgregorii*; same specimen at different focal levels, Hatchetigbee Formation, Alabama, WAH/08/077, EF T33/4.
- 3 *Platycarya platycaryoides*; Hatchetigbee Formation, Mississippi, GH00/Ht/001A, EF T25/centre.
- 4-5 *Platycaryapollenites* spp.; 4, Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF V36/centre; 5, Tallahatta Formation, Mississippi, GH00/Ha/088, EF N28/centre.
- 6 *Pseudoplicapollis limitata*; Tuscahoma Formation, Mississippi, GH00/AC/013, EF Q24/centre.
- 7-8 *Pseudoplicapollis serenus*; Porters Creek Formation, Alabama; 7, TUC/08/007, EF P23/4; 8, TUC/08/003, EF P30/3.
- 9-10 *Thomsonipollis magnificus*; same specimen at different focal levels, Nanafalia Formation, Mississippi, GH00/AC/006, EF W24/3.
- 11 "*Thomsonipollis* cf. *T. expolita*" of Frederiksen 1979; Calvert Bluff Formation, Texas, WCM/08/030, EF K29/4.
- 12 *Trivestibulopollenites* spp.; Calvert Bluff Formation, Texas, UCB/08/005, EF R28/centre.
- 13 *Trudopollis plenus*; Tuscahoma Formation, Alabama, GH08/Wa/024, EF F27/centre.
- 14 "*Trudopollis* sp. B" of Tschudy 1975; Calvert Bluff Formation, Texas, SM/08/001, EF X29/1.
- 15 *Alnus scotica*; Naheola Formation, Alabama, WAH/08/011, EF G29/4.
- 16-17 *Alnus verus*; same specimen at different focal levels, Hatchetigbee Formation, Alabama, WAH/08/069, EF P30/centre.
- 18 *Celtis tschudyi* group of Frederiksen 1988; Zilpha Formation, Mississippi, HAC/08/004, EF P23/centre.
- 19 *Compositoipollenites* sp. 1; Nanafalia Formation, Alabama, GH08/Wa/010, EF F31/4.
- 20 *Compositoipollenites* sp. 2; Tallahatta Formation, Mississippi, GH00/Ha/083, EF H29/4.
- 21 *Juglans nigripites*; Tallahatta Formation, Mississippi, GH00/Ha/087, EF Y38/1.
- 22-23 *Malvacipollis* spp.; 22, Tallahatta Formation, Mississippi, GH00/Ha/88, EF P39/3; 23, Calvert Bluff Formation, Texas, WCM/08/024, EF W33/2.
- 24 "*Myriophyllum* sp." of Frederiksen 1980; Zilpha Formation, Mississippi, HAC/08/001, EF J32/centre.
- 25 *Polyatriopollenites stellatus*; Zilpha Formation, Mississippi, HAC/08/010, EF K19/2.
- 26-27 *Ulmipollenites krempii*; 26, triporate specimen, Tuscahoma Formation, Mississippi, GH00/AC/009, EF S16/centre; 27, pentaporate specimen, Calvert Bluff Formation, Texas, UCB/08/012, EF U23/2.
- 28 *Ulmipollenites tricostatus*; Hatchetigbee Formation, Alabama, WAH/08/068, EF X22/centre.
- 29 *Ulmipollenites undulosus*; Calvert Bluff Formation, Texas, WCM/08/023, EF T24/4.
- 30 *Chenopodipollis* spp.; Calvert Bluff Formation, Texas, UCB/08/009, EF T34/1.

PLATE 5

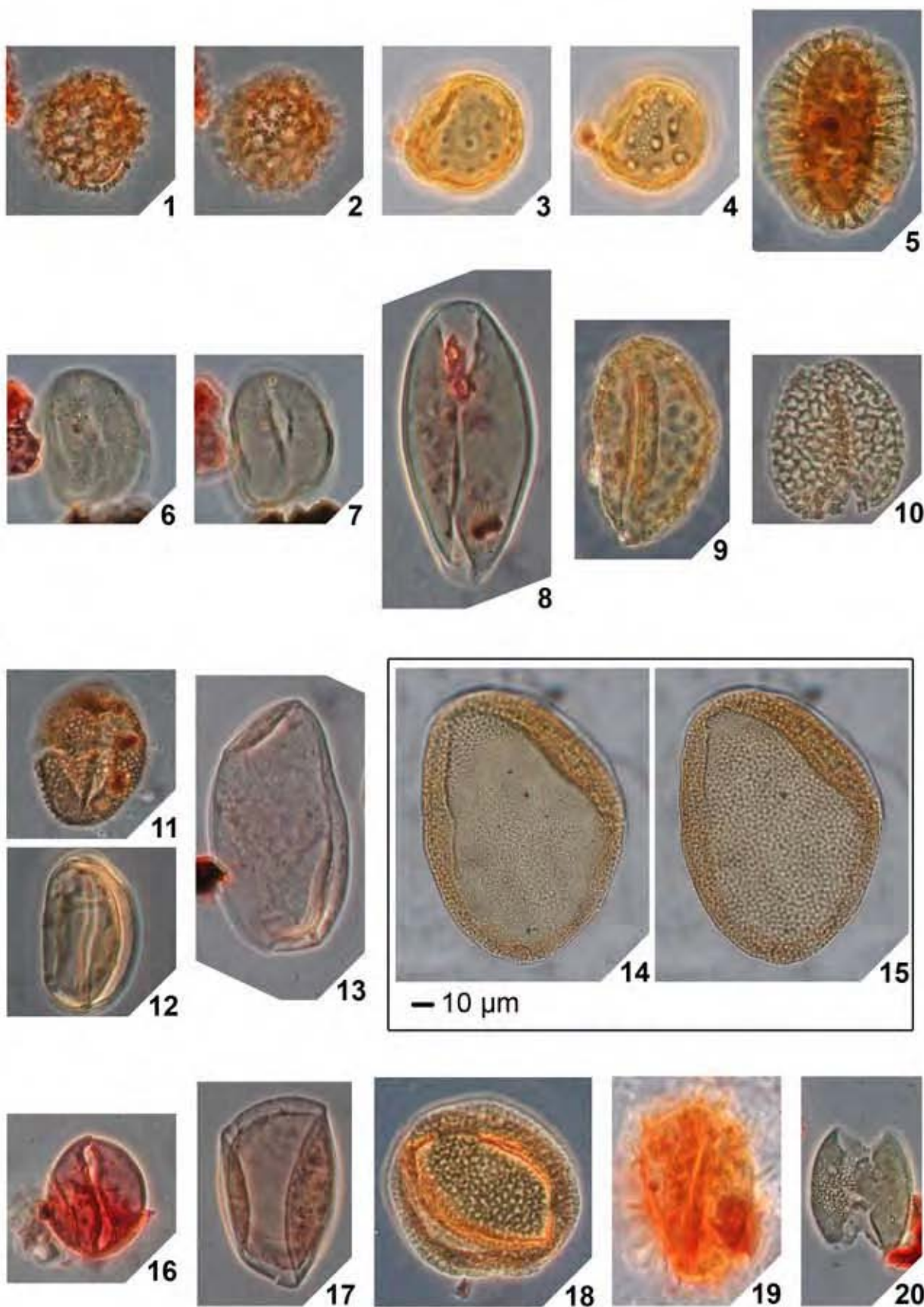


10 μ m

PLATE 6

- 1-2 *Erdtmanipollis cretaceus*; same specimen at different focal levels, Porters Creek Formation, Alabama, TUC/08/013, EF U21/3.
- 3-4 Periporate genus A; same specimen at different focal levels, Calvert Bluff Formation, Texas, WCM/08/010, EF E31/1.
- 5 *Wodehouseia spinata*; Nanafalia Formation, Alabama, GH08/Wa/009, EF O20/4.
- 6-7 *Arecipites* spp.; same specimen at different focal levels, Naheola Formation, Mississippi, JDC/08/011, EF J32/3.
- 8 *Cycadopites follicularis*; Tuscahoma Formation, Mississippi, GH00/AC/009, EF T36/centre.
- 9-11 *Liliacidites* spp.; 9, Nanafalia Formation, Alabama, GH08/Wa/011, EF R26/2; 10, Tuscahoma Formation, Mississippi, GH00/AC/008, EF V10/3; 11, Porters Creek Formation, Alabama, TUC/08/012, EF L32/3.
- 12-13 *Longapertites* spp.; 12, Hatchetigbee Formation, Mississippi, GH00/Ht/071A, EF V37/3; 13, Nanafalia Formation, Mississippi, GH00/AC/004, EF W36/3.
- 14-15 *Matanomadhiasulcites maximus*; same specimen at different focal levels, Tuscahoma Formation, Mississippi, GH00/AC/008, EF T25/2. Photographed at x400 magnification under plain light. Note the different scale bar for this taxon.
- 16 *Monocolpopollenites tranquillus*; Tuscahoma Formation, Mississippi, GH00/AC/009, EF W21/centre.
- 17 *Proxapertites* (psilate type); Nanafalia Formation, Mississippi, GH00/AC/004, EF Y25/1.
- 18 *Proxapertites* (reticulate type); Tallahatta Formation, Mississippi, GH00/Ha/88, EF J23/centre.
- 19 *Spinizonocolpites prominatus*; Calvert Bluff Formation, Texas, UCB/08/012, EF J25/centre.
- 20 *Dicolpopollis* spp.; Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF V38/1.

PLATE 6



10 μm

PLATE 7

- 1 *Acer? striatellum*; Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF W35/
centre.
- 2-3 *Cupuliferoideaepollenites* spp.; 2, Tuscahoma Formation, Mississippi, GH00/
AC/008, EF U2/2; 3, Tuscahoma Formation, Alabama, GH08/Wa/048, EF T28/2.
- 4-5 *Eucommia* spp.; 4, tricolporoidate specimen, Zilpha Formation, Mississippi,
HAC/08/001, EF L38/2; 5, tricolpate specimen, Calvert Bluff Formation, Texas,
WCM/08/030, EF R38/1.
- 6 *Foveotricolpites* sp. 1; Zilpha Formation, Mississippi, HAC/08/010, EF U28/1.
- 7 *Fraxinoipollenites* sp. 1; Tuscahoma Formation, Alabama, WAH/08/038, EF P30/
centre.
- 8 *Insulapollenites rugulatus*; Calvert Bluff Formation, Texas, UCB/08/010, EF
P36/3.
- 9 *Platanus occidentaloides*; Zilpha Formation, Mississippi, HAC/08/001, EF D24/1.
- 10-11 *Retitrescolpites anguloluminosus*; Calvert Bluff Formation, Texas, BGC/08/001,
EF D36/centre.
- 12-13 *Retitrescolpites* sp. 1; Nanafalia Formation, Mississippi, GH08/KC/017, EF M25/
centre.
- 14 “*Retitrescolpites* sp.1” of Frederiksen 1983; Hatchetigbee Formation,
Mississippi, GH00/Ht/057A, EF S32/1.
- 15 *Rousea* sp. 1; Calvert Bluff Formation, Texas, WCM/08/014, EF D18/2.
- 16 ?*Striatopollis* sp. 1; Calvert Bluff Formation, Texas, UCB/08/002, EF S40/3.
- 17 *Tricolpites asper*; Tuscahoma Formation, Mississippi, GH00/AC/012, EF Y23/4.
- 18 *Tricolpites crassus*; Tuscahoma Formation, Mississippi, GH00/AC/008, EF
V17/2.
- 19 *Tricolpites hians*; Calvert Bluff Formation, Texas, SM/08/001, EF R27/3.
- 20 *Tricolpites reticulatus*; Hatchetigbee Formation, Mississippi, GH00/Ht/036, EF
T36/3.
- 21 *Tricolpites* sp. 1; Calvert Bluff Formation, Texas, BGC/08/001, EF S30/centre.
- 22-25 *Tricolpites* sp. 2; Hatchetigbee Formation, Alabama; 22, WAH/08/072, EF T23/1;
23, WAH/08/077, EF J38/centre; 24-25, same specimen at different focal levels,
WAH/08/075, EF R27/centre.
- 26 *Tricolpites* sp. 3; Hatchetigbee Formation, Mississippi, GH00/Ht/026, EF E13/2.

PLATE 7

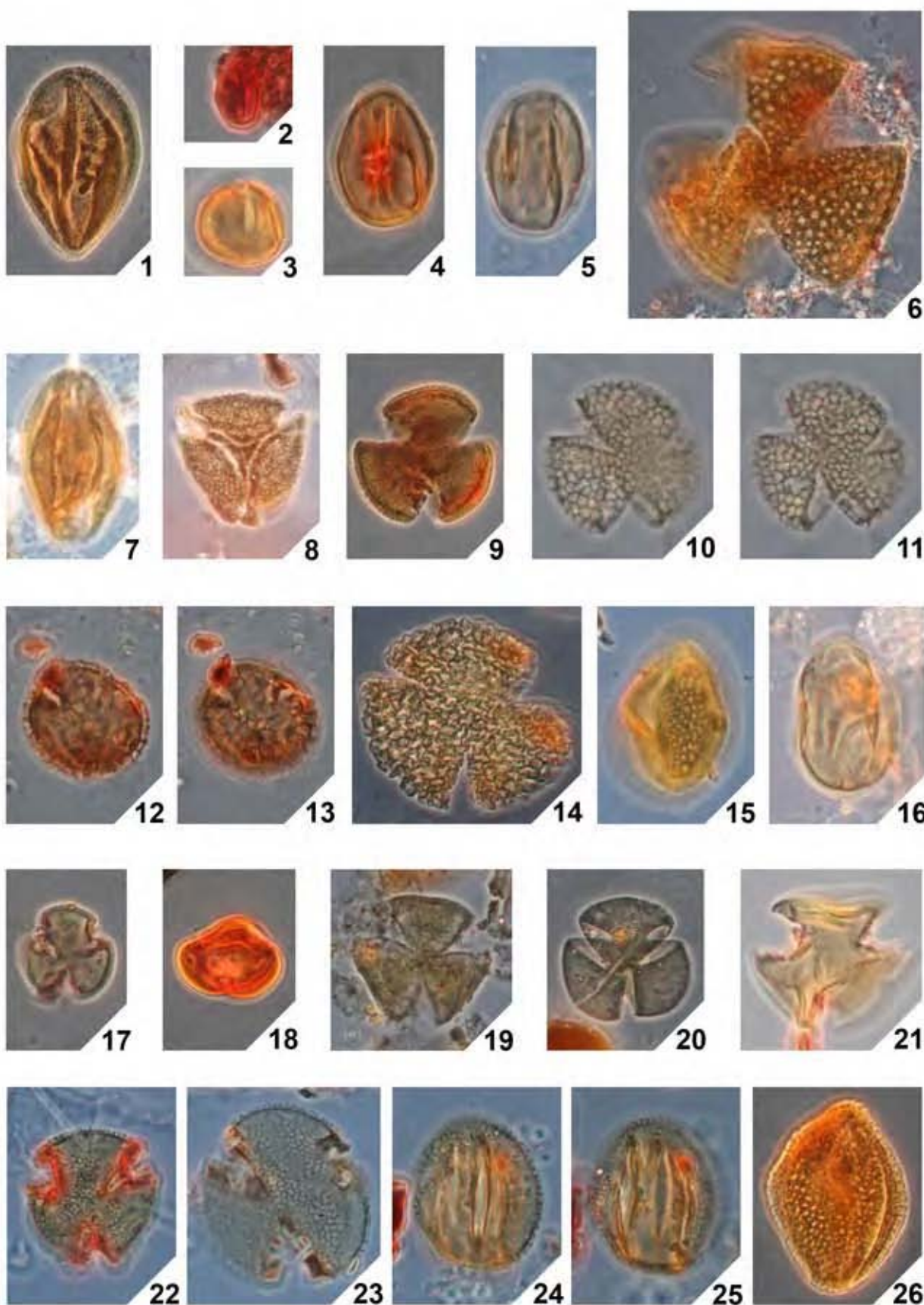
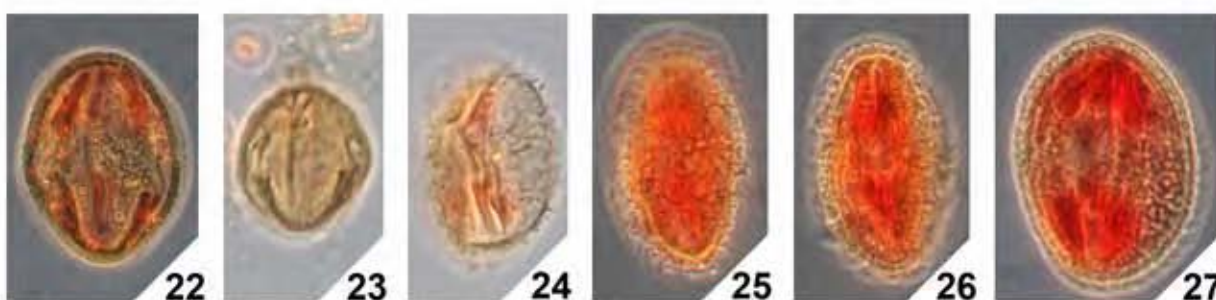
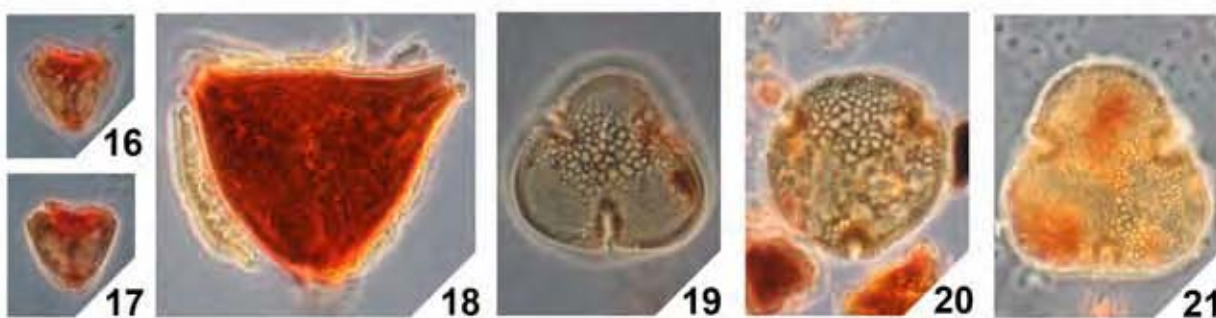
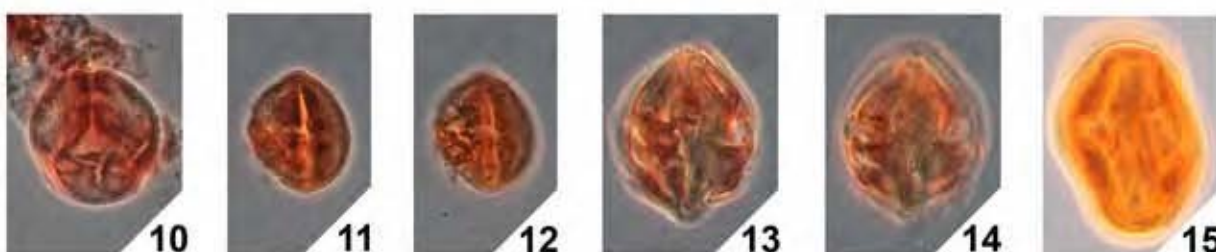
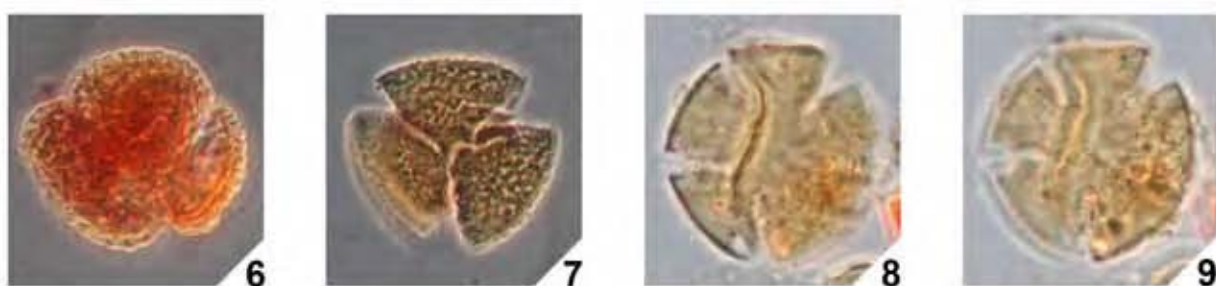
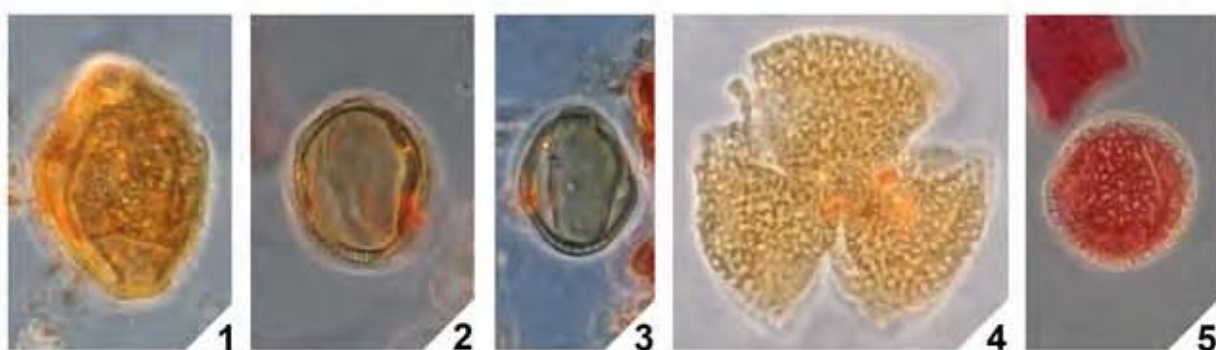


PLATE 8

- 1 *Tricolpites* sp. 3; Tusahoma Formation, Alabama, WAH/08/052, EF V34/2.
- 2-3 *Tricolpites* sp. 4; 2, Zilpha Formation, Mississippi, HAC/08/001, EF N27/3; 3, Hatchetigbee Formation, Alabama, WAH/08/079, EF V30/1.
- 4 *Tricolpites* sp. 5; Calvert Bluff Formation, Texas, UCB/08/008, EF K33/centre.
- 5-6 *Tricolpopollenites geranioides*; Nanafalia Formation, Mississippi; 5, GH00/AC/006, EF W20/centre; 6, GH00/AC/004, EF W26/4.
- 7 *Tricolpopollenites* sp. 1; Tallahatta Formation, Mississippi, GH00/Ha/085, EF S42/2.
- 8-9 Pentacolpate pollen sp. 1; same specimen at different focal levels, Calvert Bluff Formation, Texas, SM/08/001, EF W30/4.
- 10-12 *Aesculiidites circumstriatus*; 10, Tusahoma Formation, Mississippi, GH00/AC/012, EF U17/3; 11-12, same specimen at different focal levels, Nanafalia Formation, Mississippi, GH08/KC/001, EF U33/centre.
- 13-14 *Ailanthipites berryi*; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH00/Ha/089, L27/centre.
- 15 *Araliaceipollenites* sp. 1; Calvert Bluff Formation, Texas, UCB/08/002, EF E33/3.
- 16-17 *Boehlensipollis minimus*; same specimen at different focal levels, Hatchetigbee Formation, Alabama, WAH/08/069, EF H28/centre.
- 18 *Boehlensipollis verrucata*; Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF V29/1.
- 19 *Bombacacidites nacimientoensis*; Naheola Formation, Mississippi, JDC/08/037, EF M35/4.
- 20 *Bombacacidites reticulatus*; Calvert Bluff Formation, Texas, WCM/08/022, EF U23/centre.
- 21 “*Bombacacidites* sp.1” of Frederiksen 1988; Calvert Bluff Formation, Texas, UCB/08/009, EF Y34/2.
- 22 *Caprifoliipites* sp. 1; Zilpha Formation, Mississippi, HAC/08/001, EF U35/4.
- 23 *Caprifoliipites* sp. 2; Calvert Bluff Formation, Texas, SM/08/001, EF T24/4.
- 24 *Caprifoliipites* sp. 3; Calvert Bluff Formation, Texas, BGC/08/001, EF S25/centre.
- 25-26 *Caprifoliipites* sp. 4; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH00/Ha/90, EF M32/1.
- 27 *Caprifoliipites* sp. 5; Nanafalia Formation, Mississippi, GH00/AC/004, EF X12/4.

PLATE 8

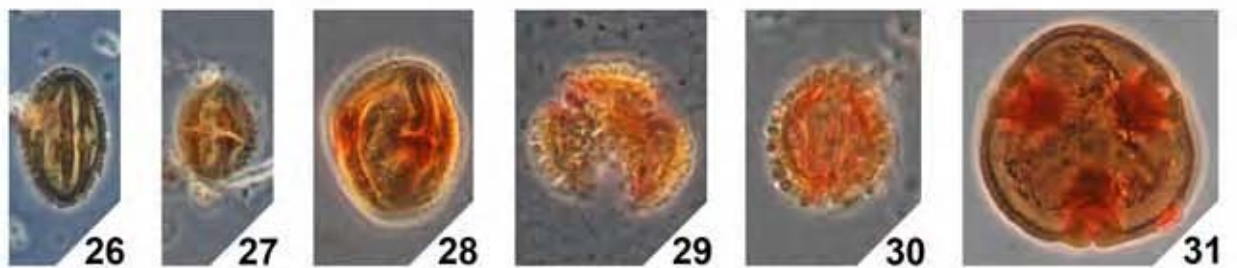
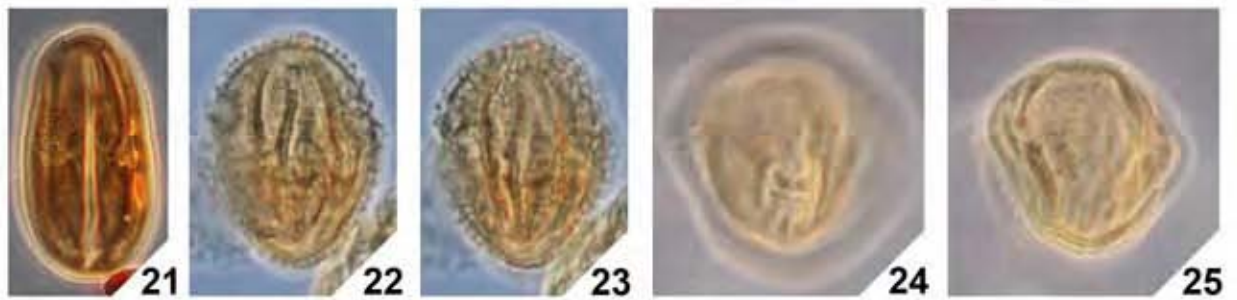
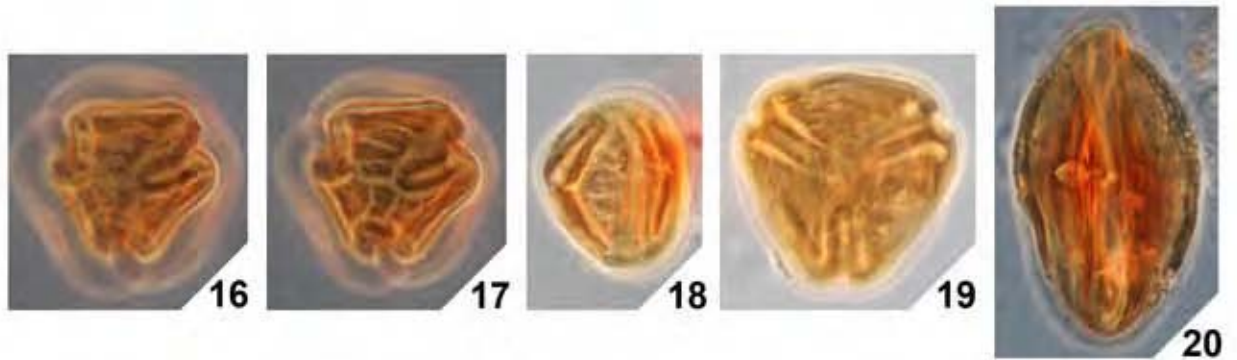
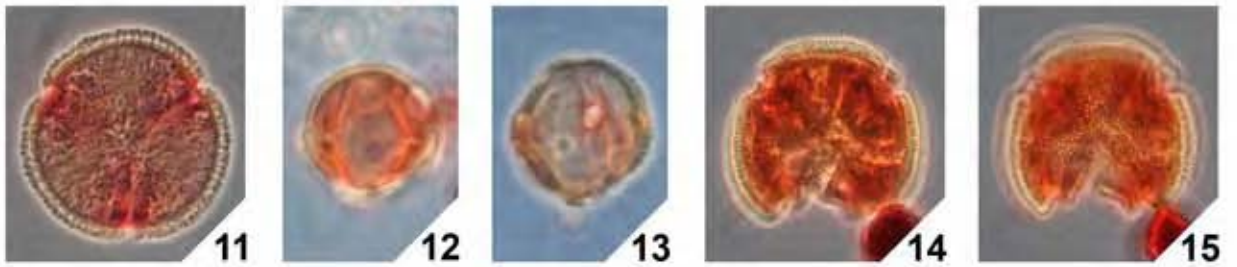
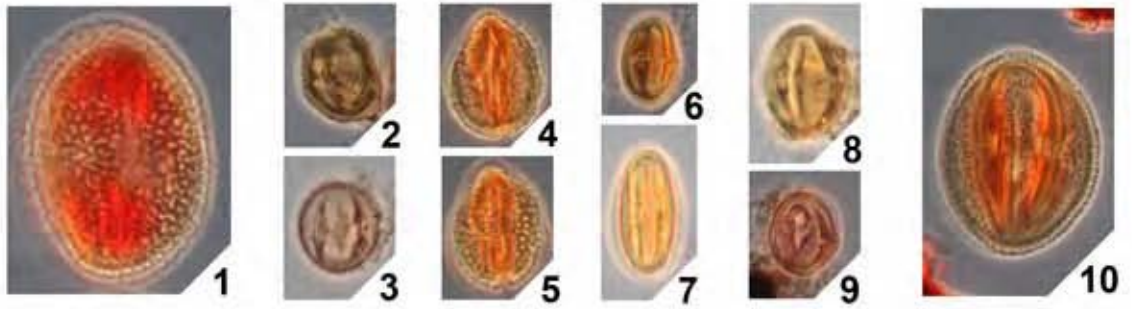


10 μ m

PLATE 9

- 1 *Caprifoliipites* sp. 5; same specimen as plate 8, figure 27, Nanafalia Formation, Mississippi, GH00/AC/004, EF X12/4.
- 2-5 *Caprifoliipites* spp.; 2, Naheola Formation, Mississippi, JDC/08/001, EF O24/4; 3, Calvert Bluff Formation, Texas, WCM/08/030, EF Y32/1; 4-5, same specimen at different focal levels, Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF R37/centre.
- 6-9 *Cupuliferoipollenites* spp.; 6, Zilpha Formation, Mississippi, HAC/08/007, EF O26/centre; 7-8, Calvert Bluff Formation, Texas, SM/08/001, 7, EF U34/4, 8, EF W32/3; 9, Tuscahoma Formation, Mississippi, GH00/AC/012, EF Z21/4.
- 10-11 *Favitricolporites baculoferus*; 10, equatorial view, Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF Y34/2; 11, polar view, Tuscahoma Formation, Mississippi, GH00/AC/009, EF X32/1.
- 12 *Favitricolporites* sp. 1; Hatchetigbee Formation, Alabama, WAH/08/066, EF M35/3.
- 13 *Favitricolporites* sp. 2; Hatchetigbee Formation, Alabama, WAH/08/066, EF S34/centre.
- 14-15 *Favitricolporites* sp. 3; Tuscahoma Formation, Mississippi, GH00/AC/011A, EF R11/3.
- 16-19 *Holkopollenites chemardensis*; 16-17, same specimen at different focal levels, Naheola Formation, Mississippi, JDC/08/037, EF O24/2; 18-19, Calvert Bluff Formation, Texas, UCB/08/009, 18, EF R22/3; 19, EF B39/4.
- 20 *Horniella brevicolpata*; Hatchetigbee Formation, Alabama, WAH/08/069, EF D34/centre.
- 21 *Horniella* sp. 1; Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF V29/centre.
- 22-23 *Horniella* sp. 2; Calvert Bluff Formation, Texas, UCB/08/007, EF U30/2.
- 24-25 *Horniella* sp. 3; Calvert Bluff Formation, Texas, UCB/08/006, EF U20/1.
- 26-28 *Horniella* spp.; 26-27, Hatchetigbee Formation, Alabama; 26, WAH/08/073, EF T33/2; 27, WAH/08/075, EF T30/3; 28, Tallahatta Formation, Mississippi, GH00/Ha/85, EF T33/1.
- 29-30 *Ilexpollenites* spp. cf. *Ilex media*; 29, Tallahatta Formation, Mississippi, GH00/Ha/088, EF T38/1; 30, Zilpha Formation, Mississippi, HAC/08/013, EF S15/2.
- 31 *Intratripoporopollenites instructus*; Zilpha Formation, Mississippi, HAC/08/001, EF F30/centre.

PLATE 9

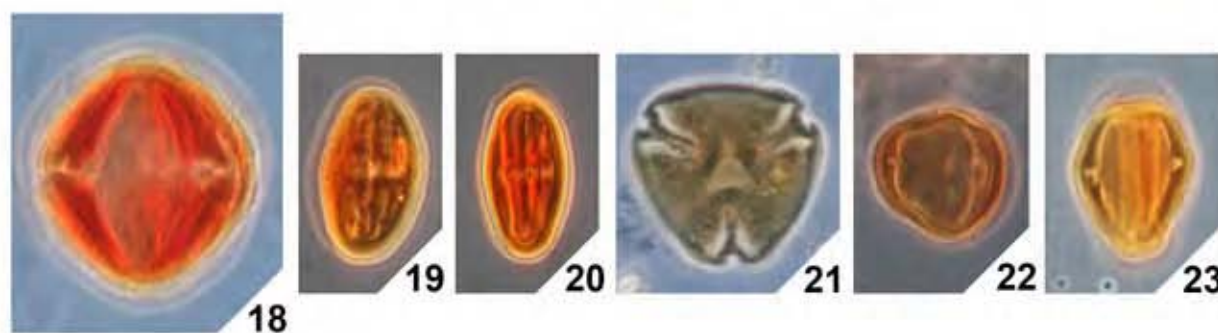
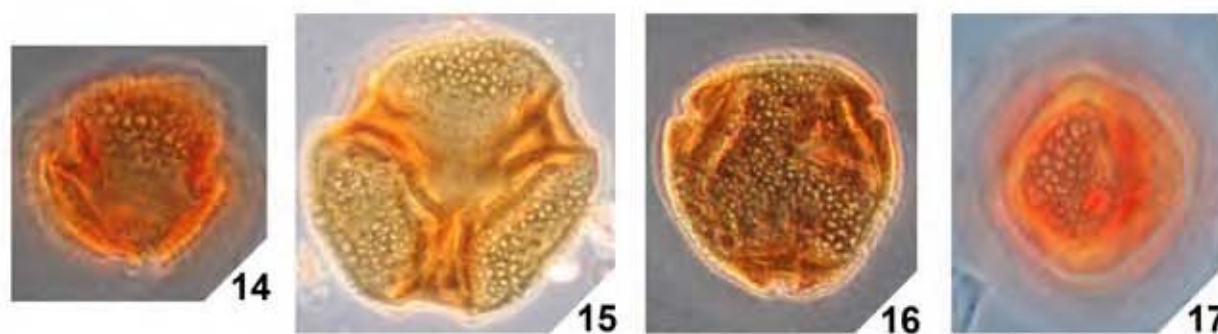
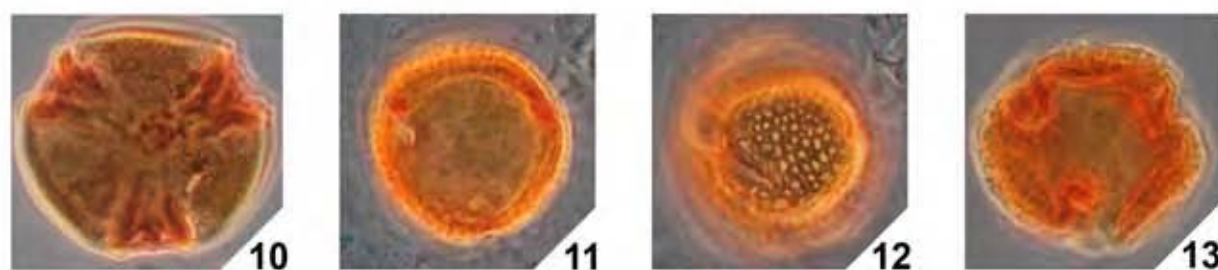
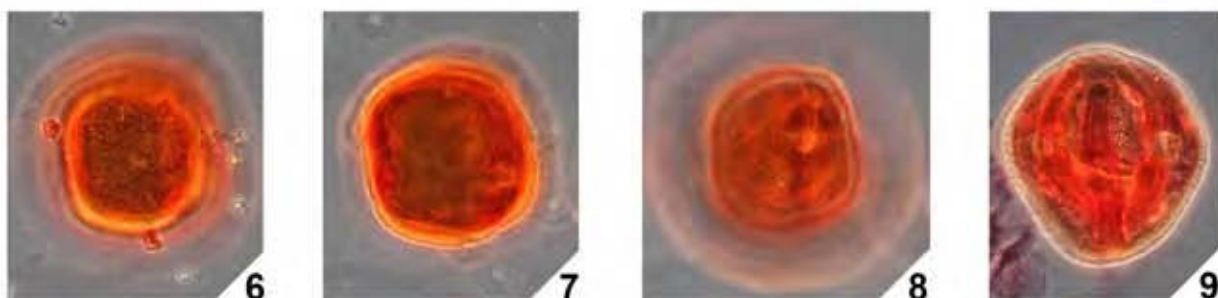
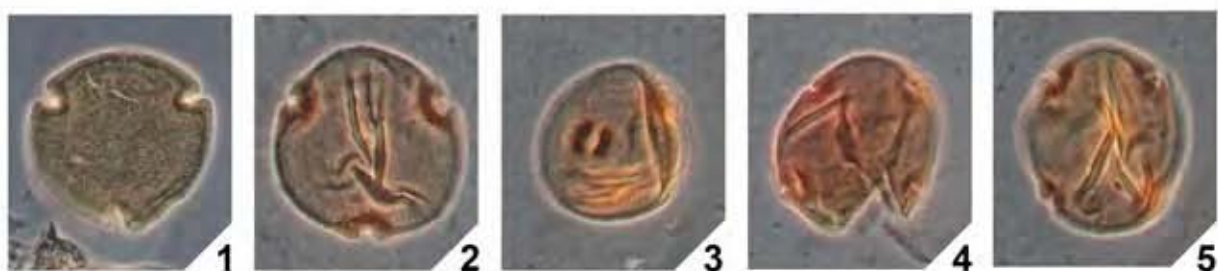


10 μ m

PLATE 10

- 1 *Intratropopollenites pseudinstructus*; Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF S12/centre.
- 2-5 *Intratropopollenites vespites*; Nanafalia Formation, Mississippi, GH00/AC/002; 2-3, tricolporate specimens, 2, EF V17/centre, 3, EF W23/centre; 4-5, tetracolporate specimens, 4, EF U29/1, 5, X26/centre.
- 6-8 *Lanagiopollis crassa* type of Frederiksen 1988; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH08/HC/045, EF K28/3.
- 9-10 *Lanagiopollis cribellata*; 9, Nanafalia Formation, Mississippi, GH00/AC/006, EF W22/3; 10, Tusahoma Formation, Mississippi, GH00/AC/11A, EF R23/4.
- 11-12 *Lanagiopollis eocaenica* type of Frederiksen 1988; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH00/Ha/89, EF X19/4.
- 13-14 *Lanagiopollis hadrodictya*; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH08/HC/046, EF N30/centre.
- 15 *Lanagiopollis lihoka*; Calvert Bluff Formation, Texas, UCB/08/010, EF X28/2.
- 16 *Lanagiopollis* sp. 1; Tusahoma Formation, Mississippi, GH00/AC/011A, EF U33/3.
- 17-18 *Lanagiopollis* sp. 2; Hatchetigbee Formation, Alabama, WAH/08/066, EF O22/2.
- 19 *Nuxpollenites crockettensis*; Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF W18/2.
- 20 *Nuxpollenites psilatus*; Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF V11/4.
- 21-23 *Nyssa kruschii* group; 21, polar view, Calvert Bluff Formation, Texas, UCB/08/006, EF N37/4; 22-23, equatorial views, 22, Tallahatta Formation, Mississippi, GH08/HC/046, N30/1; 23, *Rhoipites angustus* type, Tusahoma Formation, Alabama, GH08/Wa/048, EF W24/centre.

PLATE 10

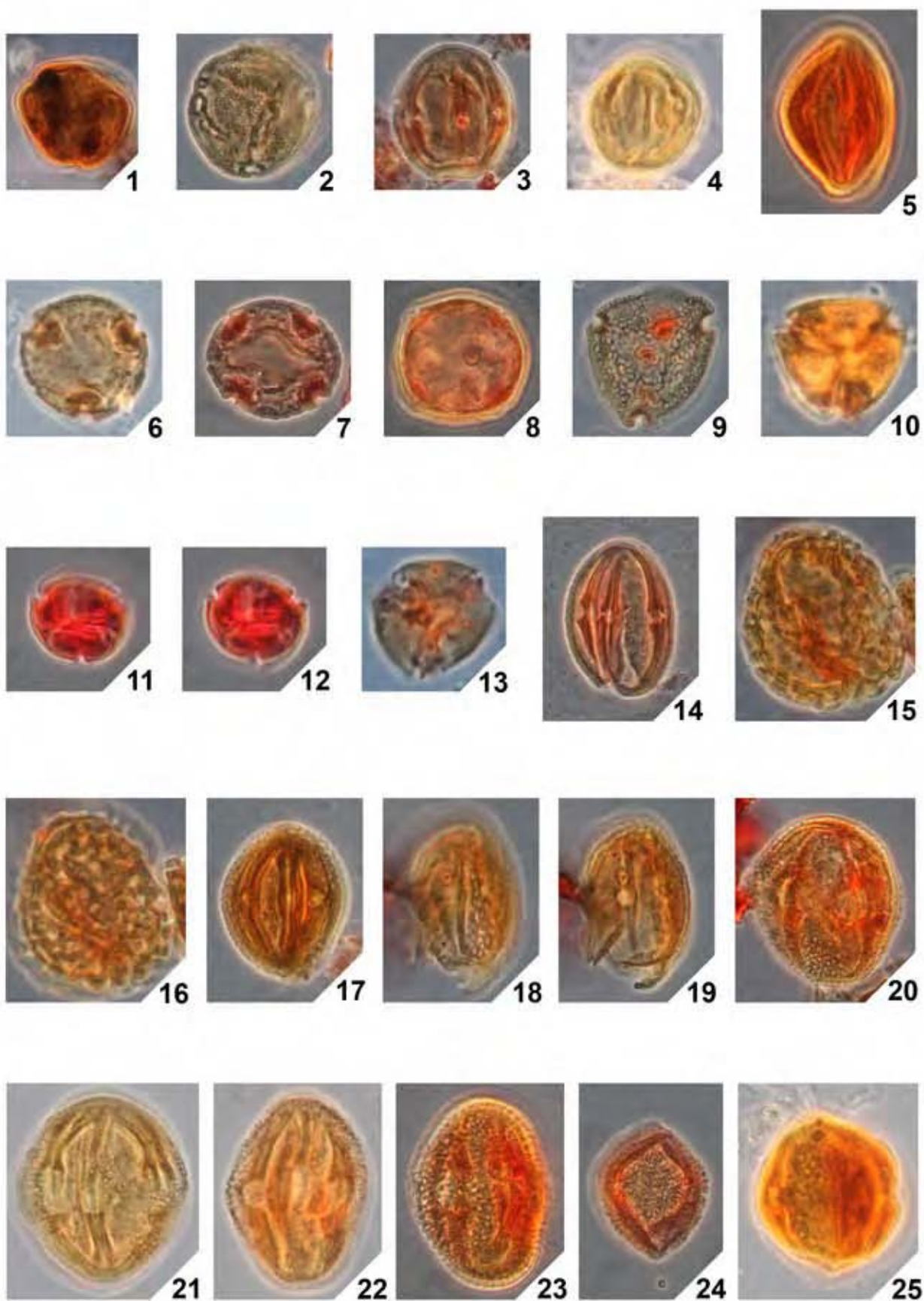


10 μ m

PLATE 11

- 1 *Nyssapollenites paleocenicus*; Porters Creek Formation, Alabama, TUC/08/004, EF Q34/2.
- 2 *Nyssapollenites pulvinus*; Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF W25/centre.
- 3-5 *Nyssapollenites* spp.; 3, Tuscahoma Formation, Mississippi, GH00/AC/012, EF U24/4; 4, Calvert Bluff Formation, Texas, UCB/08/012, EF U30/centre; 5, Tuscahoma Formation, Mississippi, GH00/AC/013, EF Y17/centre.
- 6-8 *Porocolpopollenites ollivierae*; 6, tricolporate specimen, Tuscahoma Formation, Alabama, GH08/Wa/048, EF S18/2; 7-8, tetracolporate specimens, 7, Hatchetigbee Formation, Mississippi, GH00/Ht/071A, EF S25/2; 8, Tallahatta Formation, Mississippi, GH00/Ha/90, EF N18/2.
- 9 *Porocolpopollenites* sp. 1; Nanafalia Formation, Alabama, GH08/Wa/007, EF R33/2.
- 10 *Porocolpopollenites* sp. 2; Tuscahoma Formation, Alabama, WAH/08/037, EF S17/3.
- 11-12 *Porocolpopollenites* sp. 3; same specimen at different focal levels, Tuscahoma Formation, Mississippi, GH00/AC/009, EF S38/3.
- 13 *Ranunculacidites* sp. 1; Hatchetigbee Formation, Alabama, WAH/08/067, EF J18/4.
- 14 *Rhoipites bradleyi*; Nanafalia Formation, Mississippi, GH00/AC/002, EF W20/2.
- 15-16 *Rhoipites capax*; same specimen at different focal levels, Zilpha Formation, Mississippi, HAC/08/001, EF T25/centre.
- 17 *Rhoipites cryptoporus*; Nanafalia Formation, Alabama, GH08/Wa/006, EF O26/2.
- 18-19 *Rhoipites latus*; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH08/Hc/047, EF N34/3.
- 20-23 *Rhoipites* sp. 1; 20, Tuscahoma Formation, Mississippi, GH00/AC/011A, EF R31/centre; 21-22, Calvert Bluff Formation, Texas, WCM/08/012, 21, EF Q23/4, 22, EF U24/1; 23, Tallahatta Formation, Mississippi, GH00/Ha/83, EF M24/1.
- 24 *Rhoipites* sp. 2; Tallahatta Formation, Mississippi, GH00/Ha/90, EF T18/1.
- 25 *Rhoipites* sp. 3; Calvert Bluff Formation, Texas, WCM/08/016, EF R33/centre.

PLATE 11

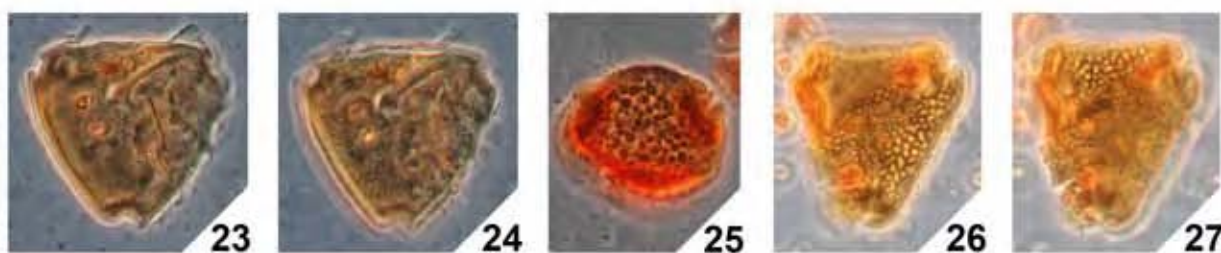
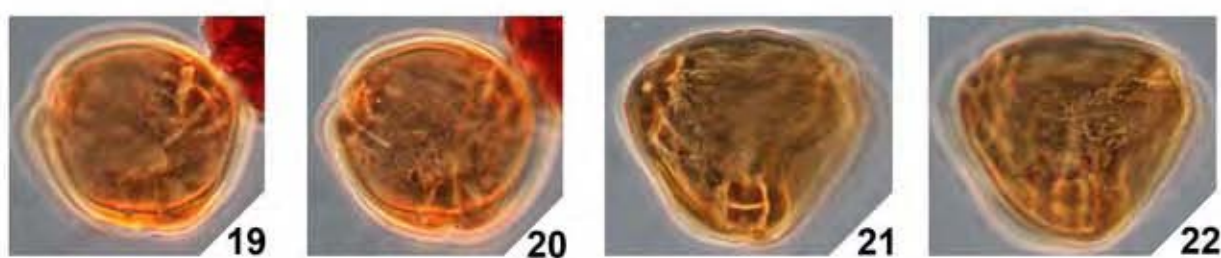
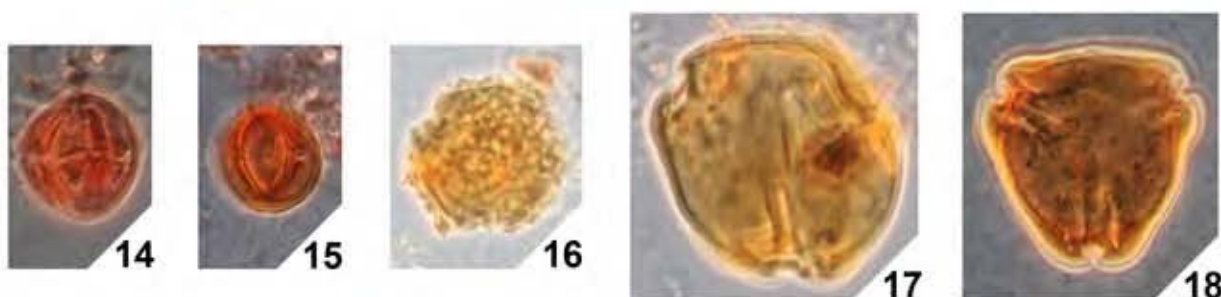
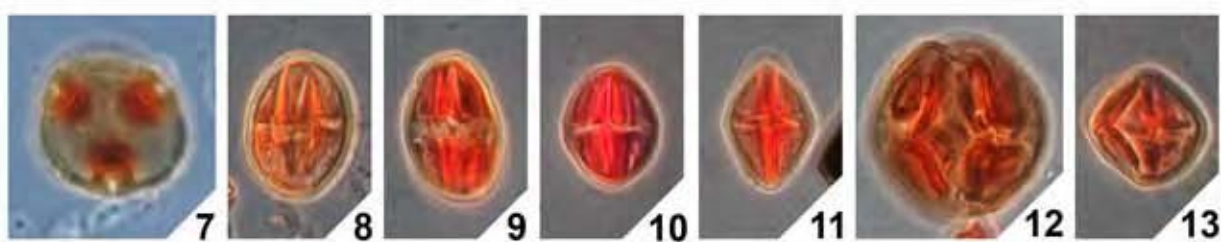
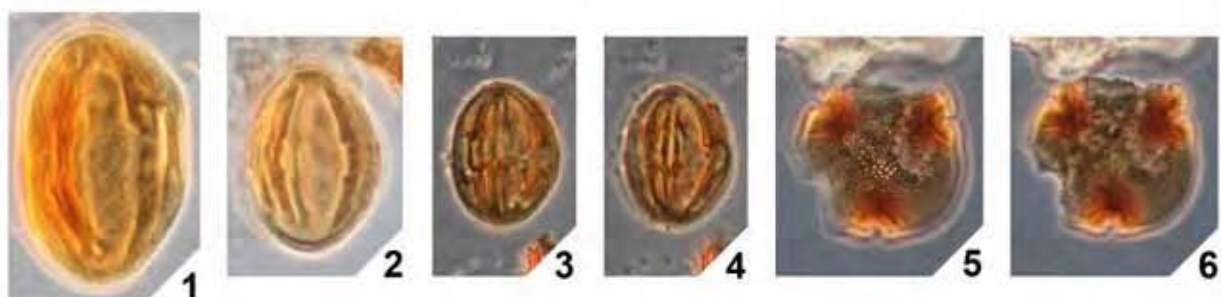


10 μ m

PLATE 12

- 1-2 *Rhoipites* sp. 4; Calvert Bluff Formation, Texas; 1, WCM/08/024, EF U20/3; 2, SM/08/001, EF V38/centre.
- 3-4 *Rhoipites* sp. 5; same specimen at different focal levels, Zilpha Formation, Mississippi, HAC/08/007, EF F20/centre.
- 5-7 *Sandiegopollis* sp. 1; 5-6, same specimen at different focal levels, Hatchetigbee Formation, Mississippi, GH00/Ht/074, EF U28/centre; 7, Hatchetigbee Formation, Alabama, WAH/08/071, EF Q38/2.
- 8-11 "*Siltaria* cf. *S. scabriextima*" of Frederiksen 1980; 8, Tallahatta Formation, Mississippi, GH00/Ha/88, EF L33/1; 9-11, Tuscahoma Formation, Mississippi; 9, GH00/AC/008, EF J6/2; 10, GH00/AC/009, EF W12/centre; 11, GH00/AC/008, EF V10/1.
- 12-15 *Siltaria-Cyrrillaceaepollenites* Complex; 12, Nanafalia Formation, Mississippi, GH08/KC/020, EF K35/1; 13-14, Tuscahoma Formation, Mississippi; 13, GH00/AC/013, EF X17/centre; 14, GH00/AC/012, EF Z26/2; 15, Zilpha Formation, Mississippi, HAC/08/010, EF N27/2.
- 16 *Spinaepollis spinosa*; Calvert Bluff Formation, Texas, UCB/08/011, EF M19/centre.
- 17-22 "*cf. Symplocoipollenites* sp." of Elsik 1968; 17, Calvert Bluff Formation, Texas, UCB/08/001, EF N34/centre; 18-20, Tuscahoma Formation, Mississippi, GH00/AC/013, 18, EF X34/2, 19-20, same specimen at different focal levels, EF X25/4; 21-22, same specimen at different focal levels, Nanafalia Formation, Alabama, GH08/Wa/005, EF M19/4.
- 23-24 *Symplocos? contracta*; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH00/Ha/88, EF R35/centre.
- 25 *Symplocos? gemmata*; Zilpha Formation, Mississippi, HAC/08/013, EF J19/3.
- 26-27 *Symplocos? thalmannii*; same specimen at different focal levels, Calvert Bluff Formation, Texas, WCM/08/025, EF P27/3.

PLATE 12

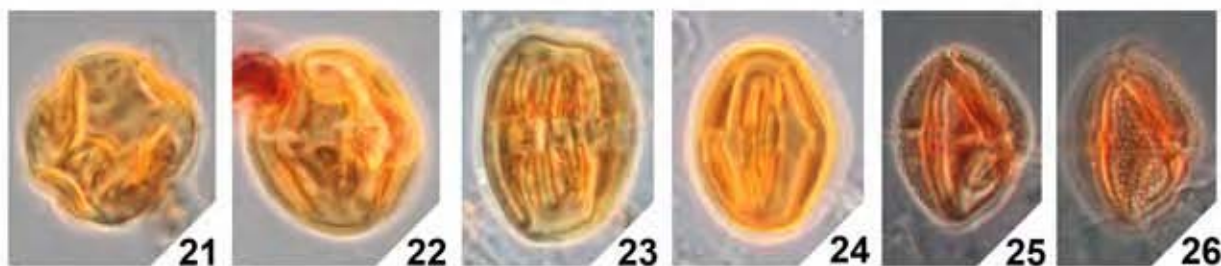
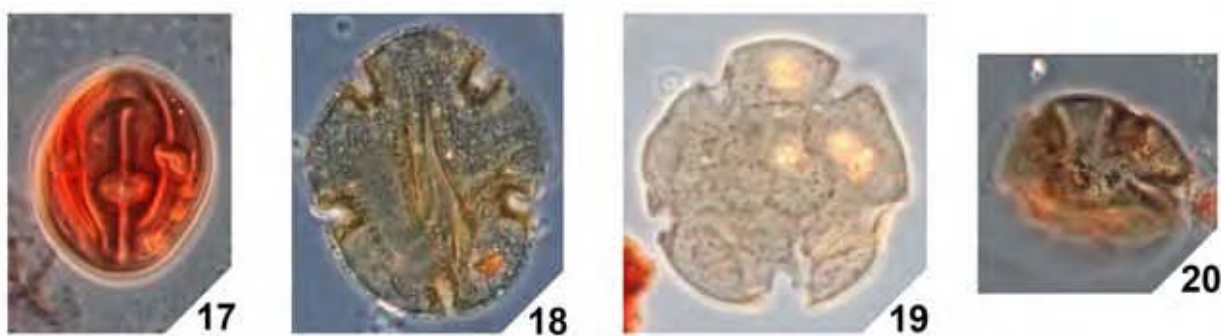
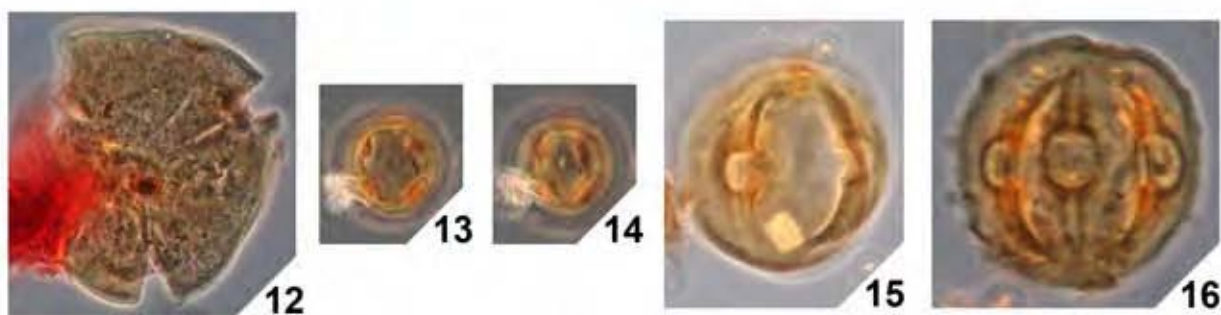
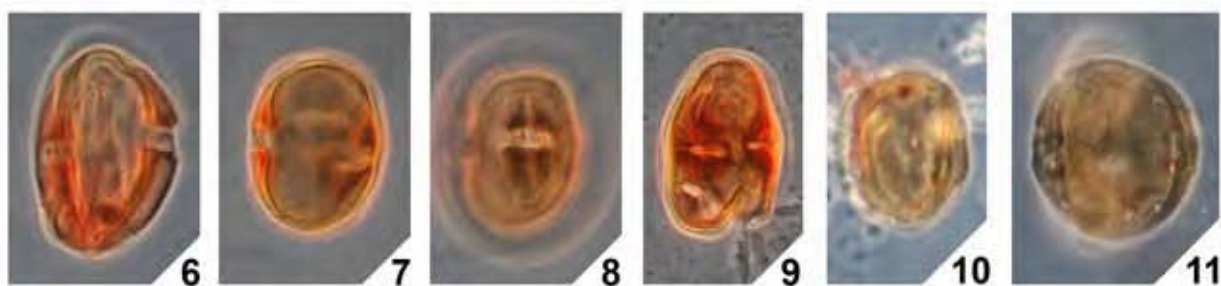
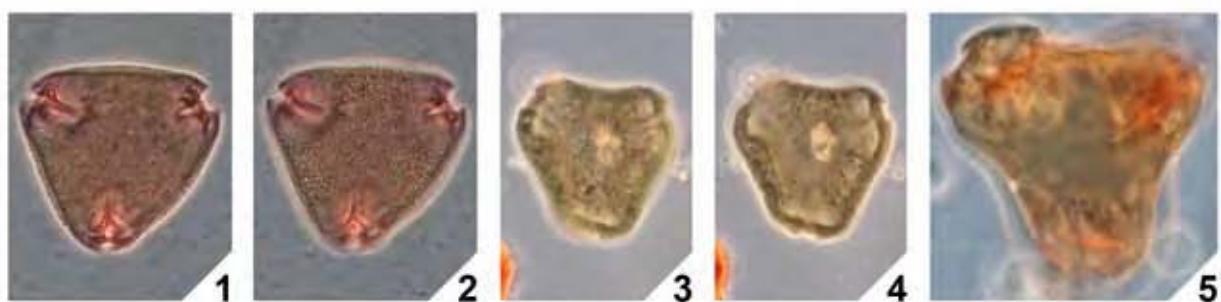


10 μ m

PLATE 13

- 1-2 *Symplocos? virginiensis*; same specimen at different focal levels, Tuscahoma Formation, Mississippi, GH00/AC/013, EF V24/3.
- 3-4 *Symplocos? sp. 1*; same specimen at different focal levels, Calvert Bluff Formation, Texas, UCB/08/007, EF U29/3.
- 5 *Symplocos? sp. 2*; Tuscahoma Formation, Alabama, GH08/Wa/046, EF S32/1.
- 6 *Tetracolporopollenites megadolium* (long colpate form); Tallahatta Formation, Mississippi, GH08/HC/047, EF W29/3.
- 7-8 *Tetracolporopollenites megadolium* (short colpate form); same specimen at different focal levels, Tallahatta Formation, Mississippi, HAC/08/024, EF R24/centre.
- 9 *Tetracolporopollenites prolatus*; Tallahatta Formation, Mississippi, GH00/Ha/088, EF T26/1.
- 10 *Tricolporopollenites sp. 1*; Tuscahoma Formation, Alabama, WAH/08/038, EF V29/centre.
- 11 *Tricolporopollenites sp. 2*; Naheola Formation, Alabama, TUC/08/023, EF J33/centre.
- 12 *Tricolporopollenites sp. 3*; Tuscahoma Formation, Mississippi, GH00/AC/011A, EF Y20/centre.
- 13-14 *Tricolporopollenites sp. 4*; same specimen at different focal levels, Naheola Formation, Mississippi, JDC/08/037, EF P21/centre.
- 15-17 "*Tricolporopollenites n. sp. A*" of Tschudy 1973; 15-16, Calvert Bluff Formation, Texas, WCM/08/012, 15, EF O30/centre, 16, EF G26/2; 17, Tuscahoma Formation, Mississippi, GH00/AC/013, EF W34/1.
- 18 *?Bombacacidites sp. 1*; Hatchetigbee Formation, Alabama, WAH/08/075, EF S22/centre.
- 19 Pentacolporate pollen sp. 1; Hatchetigbee Formation, Mississippi, GH00/Ht/001A, EF T23/3.
- 20 *Porocolpopollenites sp. 4*; Nanafalia Formation, Mississippi, GH08/KC/020, EF T20/centre.
- 21-24 *Quadrapollenites vagus*; Calvert Bluff Formation, Texas; 21, polar view, WCM/08/012, EF U37/1; 22-24, equatorial views, 22, WCM/08/012, EF R26/3; 23-24, UCB/08/010, 23, EF O26/4, 24, EF R36/2.
- 25-26 *Retistephanocolporites sp. 1*; same specimen at different focal levels, Hatchetigbee Formation, Mississippi, GH00/Ht/047, EF R11/4.

PLATE 13

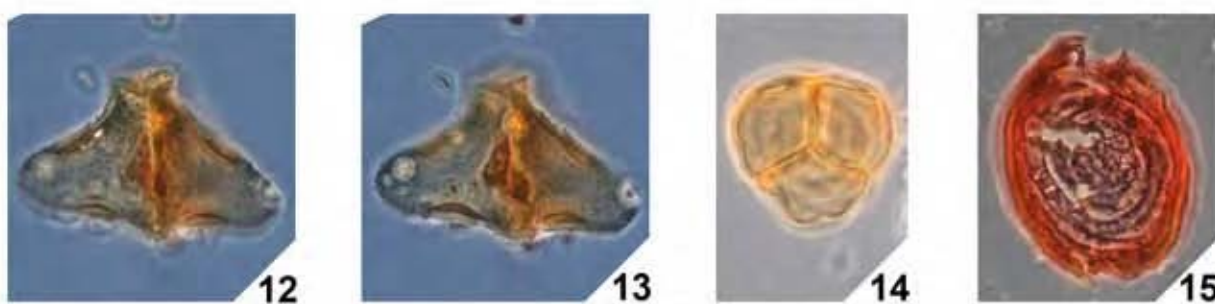
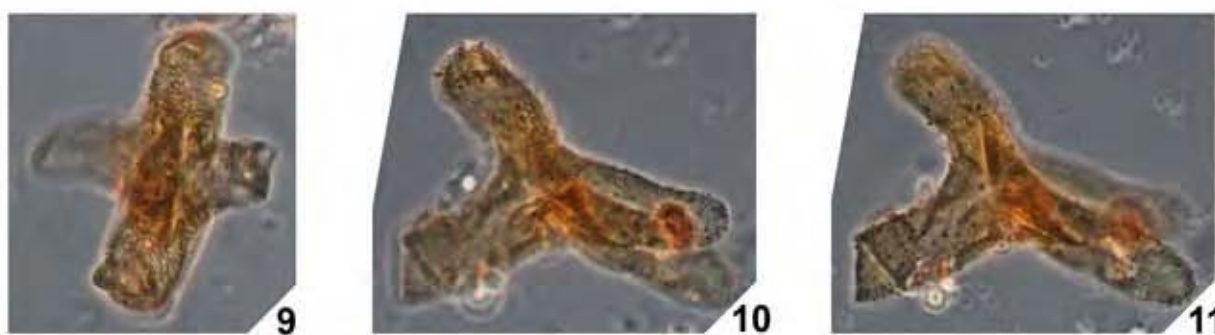
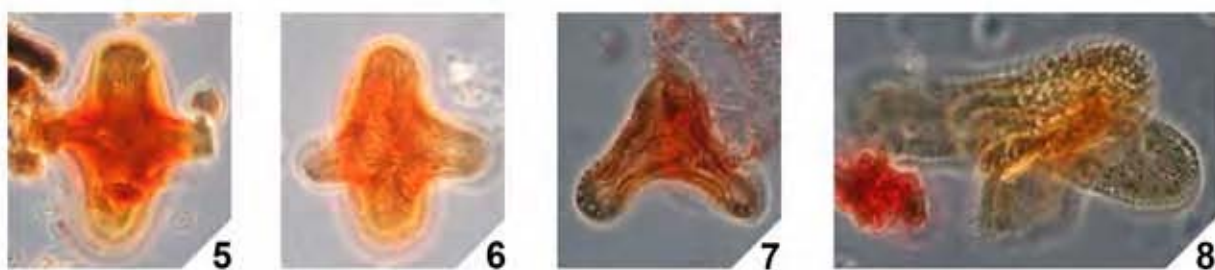
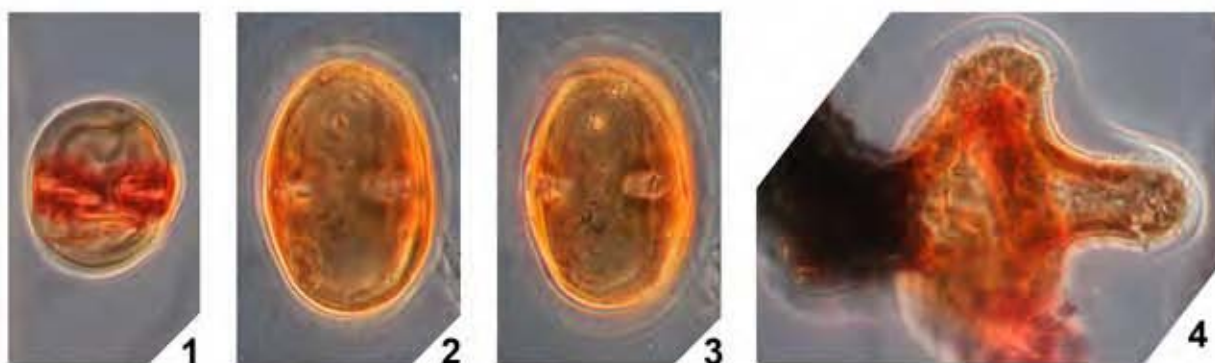


10 μ m

PLATE 14

- 1 *Tetracolporopollenites brevis*; Tuscahoma Formation, Mississippi, GH00/AC/008, EF V21/1.
- 2-3 *Tetracolporopollenites lesquereuxianus*; same specimen at different focal levels, Tallahatta Formation, Mississippi, GH00/Ha/088, EF K25/1.
- 4 *Aquilapollenites attenuatus*; Tuscahoma Formation, Mississippi, GH00/AC/008, EF S28/centre.
- 5 *Aquilapollenites* sp. 1; Calvert Bluff Formation, Texas, WCM/08/032, EF U33/1.
- 6 *Aquilapollenites* sp. 2; Calvert Bluff Formation, Texas, UCB/08/010, EF U28/centre.
- 7 *Aquilapollenites* sp. 3; Porters Creek Formation, Alabama, TUC/08/016, EF H36/centre.
- 8 *Aquilapollenites* sp. 4; Nanafalia Formation, Alabama, GH08/Wa/011, EF U29/1.
- 9 *Aquilapollenites* sp. 5; Nanafalia Formation, Mississippi, GH08/KC/020, EF F25/1.
- 10-11 *Aquilapollenites* sp. 6; same specimen at different focal levels, Nanafalia Formation, Alabama, GH08/Wa/011, EF S37/2.
- 12-13 *Aquilapollenites* sp. 7; same specimen at different focal levels, Hatchetigbee Formation, Alabama, WAH/08/077, EF O20/4.
- 14 *Ericipites* spp.; Calvert Bluff Formation, Texas, UCB/08/010, EF S27/centre.
- 15 *Pseudoschizaea* sp.; Porters Creek Formation, Alabama, TUC/08/008, EF R24/4.

PLATE 14



10 μm

CHAPTER 5: THE RED HILLS MINE PALYNOFLORA: A DIVERSE SWAMP ASSEMBLAGE FROM THE LATE PALEOCENE OF MISSISSIPPI

5.1 Introduction

The Paleocene (65.5 – 55.8 Ma) (Gradstein et al., 2004) strata of the GCP contain a well-preserved pollen and spore record, which has received decades of study (Jones, 1961; Elsik, 1968a,b; Tschudy, 1973b; 1975; Christopher et al., 1980; Frederiksen, 1991; 1994b; 1998; Harrington, 2001; Harrington and Kemp, 2001; Harrington and Jaramillo, 2007; Harrington, 2008). During the Late Paleocene the GCP experienced mean annual temperatures of $\approx 27^{\circ}\text{C}$ (Wolfe and Dilcher, 2000), and a diverse, paratropical vegetation type developed on the coastal plain. This flora consisted of a mixture of plant families with modern temperate to subtropical/tropical distributions (Jones, 1961; Harrington and Jaramillo, 2007; Harrington, 2008). The Gulf Coast flora was a geographically constrained ‘island’ ecosystem (Harrington, 2004; Harrington and Jaramillo, 2007), which was substantially different from other regions of North America (Harrington, 2003b; 2004), and South America (Jaramillo and Dilcher, 2001; Harrington and Jaramillo, 2007). The Gulf Coast sporomorph (pollen and spore) record can be used as a proxy for reconstructing vegetational changes during the Paleocene. This allows for testing of hypotheses concerning the responses of highly diverse, warm-adapted plant communities to environmental changes over extended periods of time.

Although most previous studies on the Gulf Coast sporomorphs have focused on marginal marine deposits (e.g., Tschudy, 1973b; 1975; Frederiksen, 1991; 1998;

Harrington, 2001; Harrington and Kemp, 2001; Harrington and Jaramillo, 2007), lignites are present also which represent episodes of regression, delta progradation, and the establishment of interdistributary swamp communities (Nichols and Traverse, 1971; Mancini and Tew, 1995; Thomson, 1995). Forested swamp palynofloras are of particular interest because they are dominated by sporomorphs from the local vegetation (Traverse, 1988; Moore et al., 1991; Nichols and Pocknall, 1994; Nichols, 1995), as opposed to the regional signal contained in marginal marine sediments (Haberle and Maslin, 1999; Colinvaux and De Oliveira, 2001). Hence, swamp deposits can contain a subtly different flora from the composite mixture found in marginal marine or fluvial facies (Jaramillo et al., 2007; Harrington, 2008).

The Red Hills Mine in Ackerman, Mississippi (Fig. 5.1), contains lignite seams that represent peat accumulation in coastal swamps during the Late Paleocene (c. 57-56.5 Ma). In this chapter I document the composition of the lignite-forming plant communities. Many previous studies of the Paleocene Gulf Coast sporomorph record have considered just a restricted group within an assemblage (e.g., Tschudy, 1973b; 1975; Frederiksen and Christopher, 1978), or just those taxa that are relevant to biostratigraphy (Frederiksen, 1980b; 1991; 1998). Recording all the taxa present in an assemblage is of great importance for gauging biodiversity in deep time, especially given the increasing need to document more fully the spatial and temporal patterns of biodiversity. I therefore take the approach of including all observed taxa in the sample count, to address the following questions: What is the potential taxonomic diversity when all taxa are recorded, and what is the degree of undersampling of these paratropical deposits?

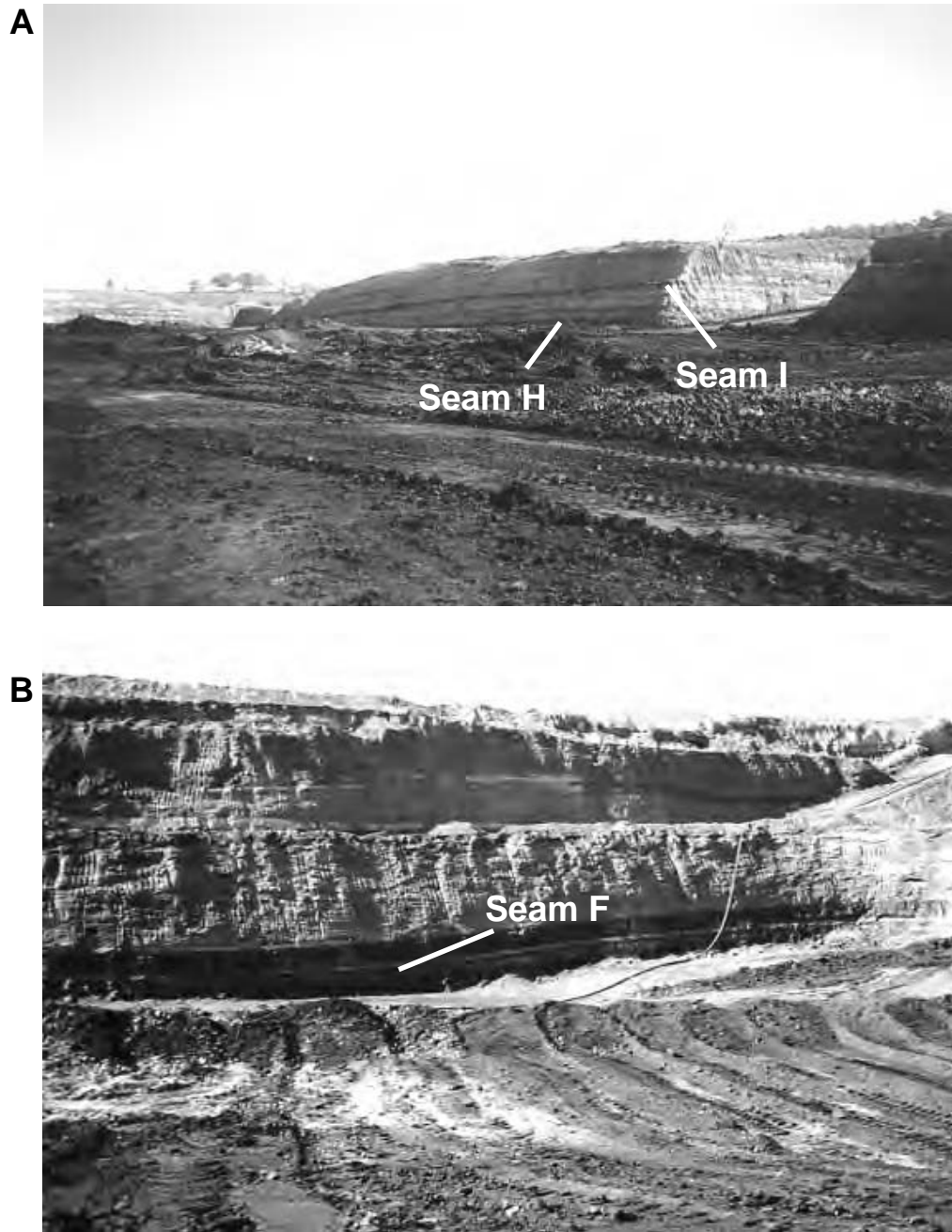


Figure 5.1. Typical exposures of lignite beds in the Red Hills Mine. A) Photograph of the south face of the mine, showing uppermost lignite seams (H and I); B) photograph of the west face of the mine, showing lignite seam F.

5.2 Geological setting

The Red Hills Mine is situated in mid central Mississippi (see Chapter 3 and Fig. 3.1) and forms a commercial source of lignite for the energy production in Mississippi. The Late Paleocene strata of the Ackerman area were previously described by Thompson (1995). The Red Hills Mine comprises lignite seams interbedded with clays and carbonaceous muds (Figs. 3.2 and 5.1). These sediments span the boundary between the Nanafalia and Tuscahoma formations of the Wilcox Group. There are no diagnostic marine fossils (e.g., planktonic foraminifera or calcareous nannoplankton) to date the mine deposits, which if similar to other Nanafalia/Tuscahoma contacts indicate an approximate correlation within planktonic foraminiferal Zone P4 (Mancini and Tew, 1991). The Red Hills Mine lignites formed in a period of regression immediately following a highstand during the deposition of the Nanafalia Formation (Mancini and Tew, 1991). This regressive phase continued into the lower Tuscahoma Formation (Mancini and Tew, 1991; Thompson, 1995). Clay layers separating the lignite seams record cyclical flooding of these coastal swamps, related to fluctuations in water depth superimposed on the overall regressive sequence (Mancini and Tew, 1995). The lignite seams are laterally extensive (Fig. 5.1), and the extent of the quarry precluded sedimentary logging between sections, which were too high and steep for detailed examination. However, a schematic stratigraphic profile is provided in Figure 3.2, based on field observations and wireline logs of the area (Thompson, 1995).

5.3 Materials and methods

Samples were collected in November 2000 from temporary exposures of lignites and associated strata in different parts of the quarry. The lignite seams are labelled by letter from the top (I) to the base (E) (Figs. 3.2 and 5.1). These samples were collected by bed number across different part of the quarry and were not collected from one stratigraphic section. All beds are traceable across the mine and are laterally persistent. In total eight samples yielded palynomorphs in sufficient quantities for counting. The dataset comprises 4370 individual grains counted from the eight samples.

5.3.1 *Rarefaction*

To standardise richness measures across the varying sample sizes and sampling intensities, rarefaction analyses were carried out. Individual-based rarefaction calculates the expected within-sample richness levels at lower sample sizes, allowing samples of different count sizes to be compared meaningfully (Gotelli and Colwell, 2001; Hammer and Harper, 2006). Sample-based rarefaction calculates the expected among-sample richness at lower sampling intensities (i.e., with lower numbers of pooled samples), and was used to compare species richness levels between lignites and non-lignites.

5.3.2 *Evenness*

Within-sample evenness was evaluated using Simpson's measure of evenness (Magurran, 2004). This is calculated by dividing the reciprocal form of the Simpson

index (the Simpson index [D] is calculated as $D = \sum p_i^2$, where p_i is the proportion of individuals in species i . The reciprocal form of the Simpson index is therefore $1/D$) by within-sample richness, so that $E_{1/D} = (1/D)/S$. Dividing by the within-sample richness converts the Simpson index from a “heterogeneity measure” (combining both the richness and evenness components of diversity) to a pure evenness measure (Magurran, 2004). This measure ranges from 0 to 1, with 0 being perfectly uneven (one taxon dominates the sample completely) and 1 being perfectly even (all taxa are equally abundant).

5.3.3 *Non-metric multidimensional scaling*

Non-metric multidimensional scaling (NMDS) was used to graphically assess compositional differences between the samples. Ordination techniques such as NMDS project complex multivariate data onto a minimal number of axes; samples that are similar in composition appear close to one another in ordination space, and those that are less similar appear farther away. NMDS is a non-parametric ordination technique, which uses ranked (rather than absolute) distance values to project the data into a two or three-dimensional space (ter Braak, 1995; Hammer and Harper, 2006). NMDS has a long history of use in ecological studies, and has been shown to portray intersample distances well (Kenkel and Orloci, 1986; Minchin, 1987; Clarke and Green, 1988; Shi, 1993; Bush and Brame, 2010).

NMDS was performed on the abundance data with singletons (those taxa that only occurred in one sample) removed. The raw data was standardized using the ‘Wisconsin’ double standardization (Bray and Curtis, 1957; Gauch and Scruggs 1979)

before performing the ordination. This first standardizes the species (columns in the data matrix) to their maxima, so that for each species the abundances are divided by the maximum abundance reached by that species. This gives the maximum abundance of each species a value of 1.0, and scales all other abundances within that species to it, thus equalizing the influence of rare and common taxa (van Tongeren, 1995). The samples (rows in the data matrix) are then standardized to their totals, by dividing the abundance of each taxon in a sample by the total within-sample abundance. Each taxon is then represented by its proportion within the sample, and every sample sums to 1.0. This removes the influence of sample size on the analysis (van Tongeren, 1995).

The goodness of fit between the original inter-sample distances and those in the NMDS ordination is assessed via a stress value (ter Braak, 1995; Legendre and Legendre, 1998; Hammer and Harper, 2006). This varies between 0 and 1, with 0 being a perfect fit between the two sets of inter-sample distances. A stress value of under 0.1 is considered to be very good, and stresses of over 0.3 are unacceptably high (ter Braak, 1995; Hammer and Harper, 2006).

5.4 Results

The Red Hills Mine flora contains eighty-five taxa identified from all eight samples. When rarefied to 300 specimens per sample, within-sample richness varies between seventeen and forty-two taxa per sample, with a mean richness of thirty taxa per sample (Table 5.1). The individual-based rarefaction curves (Fig. 5.2) show that none of the counts have fully saturated, and that two samples (GH00/AC/08

Table 5.1. Sample information. Samples are listed in stratigraphic order. N = count size, S = raw within-sample richness, R300 = expected within-sample richness given a count size of 300 specimens, R300 s.e. = standard deviation of the rarefaction estimate, E1/D = Simpson's measure of evenness, where $E = (1/D)/S$.

Sample	Formation	Lithology	N	S	R ₃₀₀	R ₃₀₀ s.e.	E _{1/D}
GH00/AC/013	Tuscahoma	Shale	358	36	34.23	1.21	0.21
GH00/AC/012	Tuscahoma	Lignite	302	34	33.90	0.31	0.21
GH00/AC/011A	Tuscahoma	Clastic	326	42	40.91	0.98	0.23
GH00/AC/009	Tuscahoma	Lignite	1368	29	17.76	2.04	0.05
GH00/AC/008	Tuscahoma	Clastic	390	46	42.01	1.73	0.18
GH00/AC/004	Nanafalia	Lignite	896	33	22.58	2.05	0.05
GH00/AC/002	Nanafalia	Lignite	330	27	25.98	0.95	0.19
GH00/AC/006	Nanafalia	Lignite	400	29	26.47	1.38	0.22

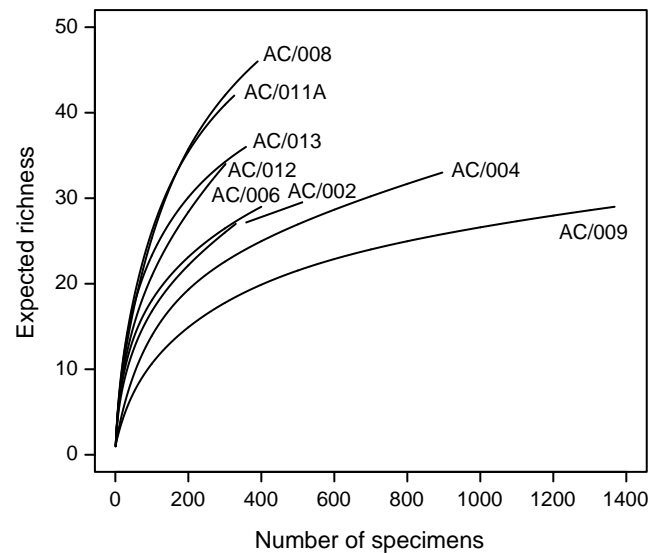


Figure 5.2. Individual-based rarefaction curves for each of the samples used in this study. Curves show the expected within-sample richness (y-axis) for a given sample size (x-axis). 95% confidence interval lines have been removed for clarity.

and GH00/AC/11A, both of which represent clay lithologies) remain undersampled. The samples have uneven abundance distributions (Table 5.1 and Fig. 5.3), with a maximum $E_{1/D}$ value of 0.23. Samples GH00/AC/04 and GH00/AC/09 are highly uneven ($E_{1/D} = 0.05$ in both cases). There are no richness or evenness trends associated with the stratigraphic position of the samples, and no change can be detected across the Nanafalia/Tuscahoma boundary (Table 5.1). The sample-based rarefaction curves (Fig. 5.4) demonstrate that when pooled together, non-lignite samples have a significantly higher among-sample richness than lignite samples. Although comparing the expected richness at lower numbers of pooled *samples*, the x-axis on Figure 5.4 has been re-scaled to the number of *specimens*, based on the mean number of specimens per sample for each curve (659.2 specimens per sample for lignites, and 358 specimens per sample for non-lignites). This ensures that species richness rather than species density is being compared (Gotelli and Colwell, 2001; Colwell et al., 2004). The shallower slope of the lignite curve compared to the non-lignite curve shows that the lignite samples are more heterogeneous in composition than the non-lignites.

The samples are dominated by angiosperms (77.6% of taxonomic groups), with spore producing plants (pteridophytes and bryophytes) and gymnosperms being of less importance (17.6% and 4.7% of taxa respectively). The majority (79%) of taxa could not be assigned to extant plant families. However, Sphagnaceae (sphagnum moss), Lycopodiaceae (club mosses), Schizaeaceae (climbing ferns), Taxodiaceae (bald cypress), Cycadaceae (cycad family), Eucommiaceae, Sparganiaceae (bur reeds), Sapotaceae (sapote family), Betulaceae/Myricaceae

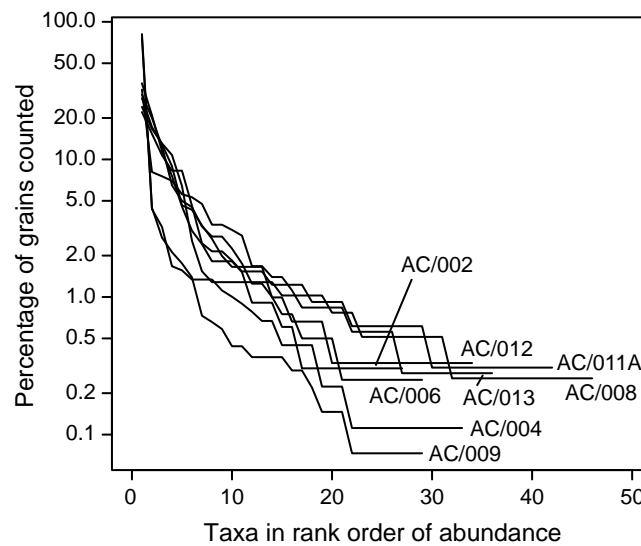


Figure 5.3. Rank/abundance plots for each of the samples used in this study. Taxa are plotted in rank order from the most abundant to the least abundant (x-axis). The y-axis represents percentage abundance of the within-sample count size, with ln scale.

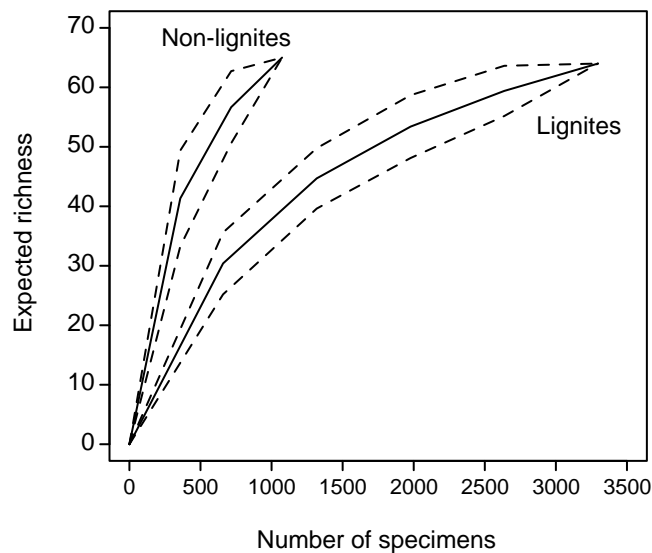


Figure 5.4. Sample-based rarefaction curves for lignite (lower solid line) and non-lignite (upper solid line) samples. Curves show the expected richness (y-axis) for a given number of pooled samples (x-axis). Dashed lines show 95% confidence intervals. The x-axis has been re-scaled to number of specimens, based on the mean number of specimens per sample for each curve (Gotelli and Colwell, 2001; Colwell et al., 2004).

(birch or sweet gales), Juglandaceae (hickory family), Arecaceae (palm family), and Cornaceae (*Nyssa*, tupelo trees) are represented in the Red Hills Mine flora.

NMDS (Fig. 5.5) demonstrates that the samples are variable both in terms of composition and relative abundance of sporomorph taxa. The five lignite samples (Table 5.1) are compositionally highly variable from one another. Sample GH00/AC/002 occurs in isolation, being dominated by spores (89% of the count, compared to 10% - 40% in all other samples). Samples GH00/AC/004 and GH00/AC/009 also occur separately, and have a close association with the Betulaceae/Myricaceae pollen type and *Favitricolporites baculoferus*. The Betulaceae/Myricaceae type is an important part of most of the samples, but constitutes >75% of the count in samples GH00/AC/004 and GH00/AC/009, which accounts for their highly uneven abundance distributions (Table 5.1 and Fig. 5.3). The non-lignite samples (GH00/AC/008, GH00/AC/011A, and GH00/AC/013) form a discrete cluster (the grey composition space in Figure 5.5). Bisaccate pollen occurs in higher abundances in the two clay samples, comprising 22% of the count in GH00/AC/11A and 24% of the count in GH00/AC/08. The pteridophytes *Laevigatosporites haardtii*, *Cicatricosisporites dorogensis*, and *Deltoidospora* sp. are abundant in all samples, and *Cupressacites hiatipites* occurs in most samples but only in very low abundances. *Thompsonipollis magnificus* is locally abundant. Each clay sample was found to contain one dinoflagellate cyst (*Spiniferites* sp. in sample GH00/AC/08; the dinoflagellate cyst in sample GH00/AC/11A could not be identified). As with richness and evenness, there are no compositional trends associated with the stratigraphic position of the samples.

Nine morphotypes were also documented that were not found in the

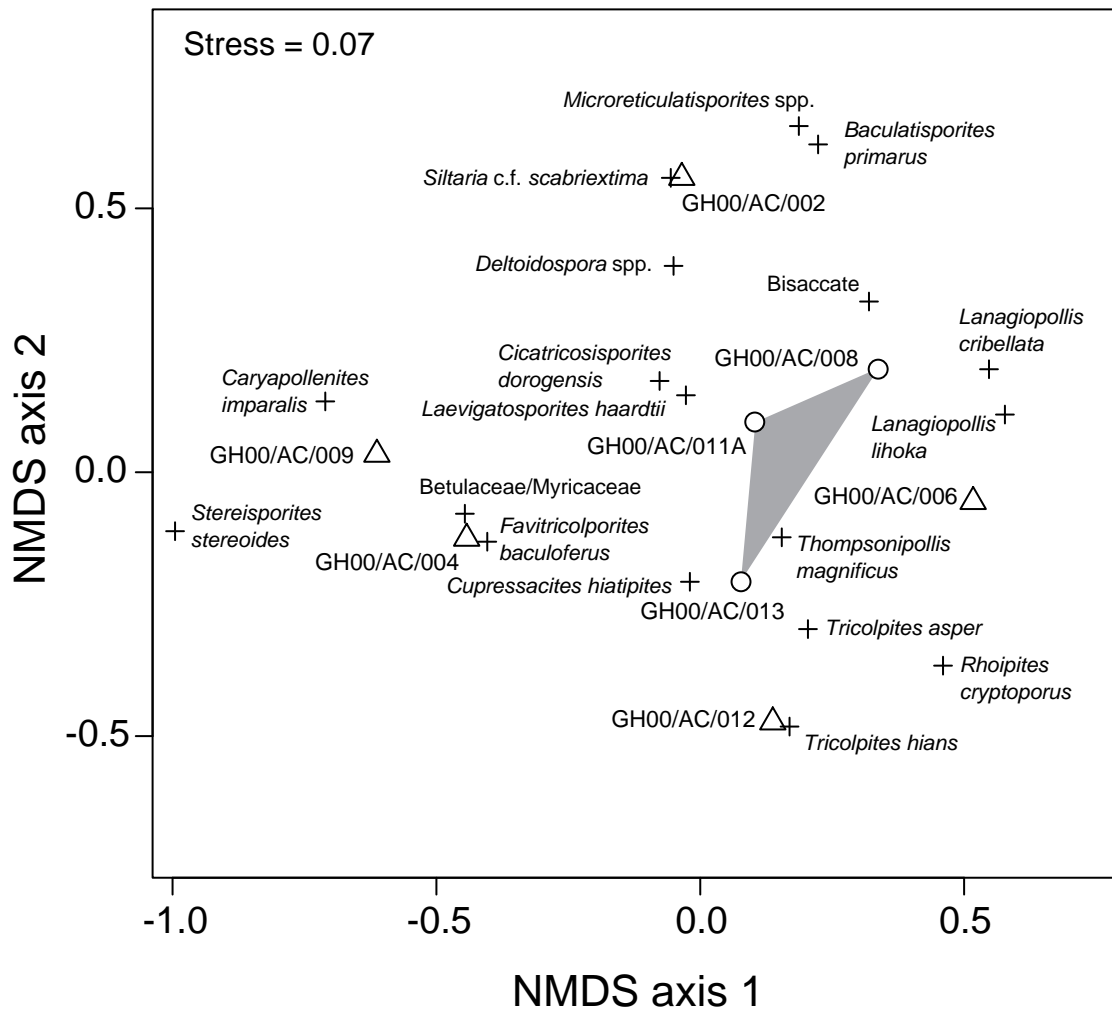


Figure 5.5. NMDS biplot of the Red Hills Mine samples, together with selected taxa. Triangles = lignite samples, circles = clastic samples (placed in grey composition space), crosses = taxa.

consulted published literature (Thompson and Pflug, 1953; Elsik, 1968a, b; Srivastava, 1972; Nichols, 1973; Tschudy, 1973a, b; 1975; Krutzsch and Vanhoorne, 1977; Frederiksen and Christopher, 1978; Nichols and Ott, 1978; Frederiksen, 1979; Christopher et al., 1980; Frederiksen, 1980a, b; Gaponoff, 1984; Frederiksen, 1988; 1991; Pocknall and Nichols, 1996; Frederiksen, 1998). These taxa were rare, with five or less specimens of each being found in the whole assemblage. These taxa are described in the Chapter 4.

5.5 Discussion

5.5.1. Environmental interpretation

The complex, heterogeneous nature of tropical swamp communities (Souza and Martins, 2005) is reflected in the compositional variability between the Red Hills Mine lignite samples (Figs. 5.4 and 5.5). The Red Hills Mine lignites are mostly indicative of an angiosperm-dominated forested coastal swamp, although sample GH00/AC/002 (the second lowest in the stratigraphic profile; Table 5.1 and Fig. 3.2) represents a more open, immature and perhaps wetter environment dominated by ferns. The great abundance of the Betulaceae/Myricaceae pollen in the lignite samples can be attributed to a probable anemophilous (wind-pollinated) habit. Although anemophilous taxa comprise only 2-3% of trees in tropical forests (Bush, 1995), pollen from these taxa are typically over-represented in pollen samples, due to the vast quantity of pollen released (Jackson, 1994; Bush and Rivera, 2001). The low abundances of sphagnum moss (less than 2% of the count in each sample) may suggest that conditions were not acidic enough for these plants to thrive (Styan

and Bustin, 1983; Clymo, 1987; Moore, 1987; Nichols and Pocknall, 1994). However, modern species of sphagnum moss frequently reproduce vegetatively (Nichols and Pocknall, 1994), implying that it may be under-represented in these samples.

The clay horizons (from which samples GH00/AC/008 and GH00/AC/011A were taken) reflect the temporary rises in sea level identified by Mancini and Tew (1995), which would have flooded the coastal swamps. The extensive lateral persistence of these clay layers, and the lack of channels or any other sedimentary features indicative of fluvial deposition, mean that a fluvial origin can be discounted. Marine palynomorphs have also been found in the two clay samples, although their extremely low abundance (one specimen per sample) implies that they may be reworked, or instead indicates very brackish water conditions. The high percentage of bisaccate pollen found in these samples suggests an allochthonous component, with these samples representing a larger source area than the lignites. In modern environments, bisaccate pollen grains are typically produced in great quantities, and are well transported by both wind and water (Faegri and van der Pijl, 1971; Nichols, 1995; van der Kaars, 2001). If they had been present in the area immediately surrounding the swamp, they would be expected to show a high level of abundance in the lignites as well as the clay horizons. The bisaccate pollen that is present possibly originated a substantial distance inland from the swamps, and was secondarily transported by rivers to the coast. The high aerodynamic and hydrodynamic efficiency of bisaccate pollen means that it is typically a dominant constituent of marginal marine sporomorph assemblages, and becomes increasingly over-represented further from the shore (Heusser and Balsam, 1977; Heusser, 1988;

Sun et al., 1999; de Vernal and Hillaire-Marcel, 2008). Sample GH00/AC/013 was taken from a carbonaceous shale horizon. This sample is similar in composition to the lignite samples, and does not contain any bisaccate pollen, suggesting that it is still dominated by autochthonous sporomorphs. I interpret this as representing a waterlogged soil horizon.

The much larger source area represented by the two clay samples suggests that a higher within-sample richness should be anticipated (Traverse, 1988), and this is supported by the almost linear relationship exhibited by the rarefaction curves (Fig. 5.2). The non-lignite samples also have a higher among-sample diversity (Fig. 5.4) and are more compositionally homogeneous than the lignite samples (Figs. 5.4 and 5.5). Changes in richness and composition are therefore tied to differing lithologies, and no trends in richness, evenness, or compositional changes related to the stratigraphic positions of the samples have been detected in the Red Hills Mine section (Table 5.1, Figs. 5.2, 5.3 and 5.5). Jaramillo et al. (2007) also found that non-coal palynofloras from the Late Paleocene of Columbia have higher richness (both within and between-sample) than coal (=swamp) palynofloras, and noted compositional differences between them.

5.5.2 Comparisons with other Late Paleocene palynofloras

Based on comparisons between Late Paleocene swamp deposits in both Texas (Wilcox Formation), and Wyoming (Tongue River Member, Fort Union Formation), Nichols (1995) noted that pollen of the gymnosperm family Taxodiaceae dominated swamps in the north, while angiosperm pollen dominated in the south. The Red

Hills Mine lignites are clearly in keeping with this trend, with angiosperm pollen dominating most samples, and taxodiaceous pollen (represented by *Cupressacites*, *hiatipites* and *Sequoiapollenites* sp.) being only rare or absent in all samples. However, Taxodiaceae pollen was found to be dominant in Late Paleocene and Early Eocene marginal marine deposits from Mississippi and Alabama (Harrington 2001; 2008), suggesting that although this taxon was not abundant in the Red Hills Mine swamps, it was an important part of the regional vegetation. There are other clear floral similarities between the Texas lignites and the Red Hills Mine, with an abundance of Betulaceae and Juglandaceae pollen also recorded in east Texas (as part of the *Corylus*-*Sphagnum* assemblage of Nichols and Traverse [1971]). The fern spore genera *Laevigatosporites* and *Cicatricosisporites* are also common in the Texas samples, as was *Thompsonipollis magnificus*. However, palm pollen is an important part of the flora in central Texas (the palm assemblage of Nichols and Traverse (1971)), whereas grains potentially assigned to Arecaceae (*Arecipites*) occur only in very low abundances in the Red Hills Mine. Palm pollen increased in relative abundance on the eastern Gulf Coast during the earliest Eocene (Harrington 2001; 2008).

Direct richness comparisons with published accounts from strata of a similar age are limited by the lack of studies with a similar rationale (i.e., counting all taxa present, not just those of stratigraphic importance). Hence, Frederiksen (1994b) calculated a standing diversity of fewer than 50 angiosperm species for the Nanafalia/Tusahoma boundary on the eastern Gulf Coast, whereas 66 angiosperm species have been recorded from the Red Hills Mine samples. Frederiksen's (1998) biostratigraphic study of the Late Paleocene of Mississippi, Alabama and western Georgia made use

of 44 angiosperm pollen taxa, of which just 27 had ranges that crossed the Nanafalia/Tuscaloosa formation boundary (Composite Section B of Frederiksen 1998). This demonstrates the degree of underestimation that would result by using data from biostratigraphic studies to estimate species richness trends, and justifies the approach taken here in constructing a new dataset based on a more comprehensive sampling scheme. It is worth noting, however, that the richness recorded in the Red Hills Mine flora is not unprecedented on the Gulf Coast, as Elsik (1968a, b) recorded ninety-nine sporomorph taxa from a lignite bed in the Late Paleocene Rockdale Formation of Texas. Elsik provided very little information concerning his sampling strategy (e.g., the number of samples studied, and the counting method employed), making more thorough comparisons with the present study impossible.

The high levels of palynological richness recorded from Late Paleocene deposits on both the eastern (Mississippi) and western (Texas) U.S. Gulf Coast suggest that plant communities at this time were more diverse than has previously been appreciated. This may mean that areas of North America were not dissimilar to the tropics during parts of the Paleogene, given the reduced latitudinal diversity gradient that has been suggested for this time (Harrington, 2004; Jaramillo et al., 2007).

5.6 Conclusions

The Red Hills Mine palynoflora represents a paratropical forest community, which developed in a coastal swamp environment on the eastern U.S. Gulf Coast. The flora is highly diverse, with eighty-five sporomorph morphospecies

recorded from the whole assemblage. Angiosperm pollen dominates (especially the Betulaceae/Myricaceae type), with pteridophyte pollen being locally abundant. Gymnosperms are generally less important, although clay layers contain a high proportion of allochthonous bisaccate pollen, which may have originated in a hinterland source area a substantial distance from the swamps. The lignite samples are variable in terms of their composition, reflecting the high spatial and temporal heterogeneity of swamp communities. Differences in diversity and composition between samples are related to lithological biases (lignite vs. non-lignite), rather than temporal trends throughout the Red Hills Mine sequence. The Red Hills Mine flora is similar compositionally to other Gulf Coast lignite deposits in Texas, although palm pollen was much more important in central Texas swamp communities than it was in Mississippi. The high diversity of these samples, coupled with the recognition of nine previously undescribed taxa, suggests Gulf Coast sporomorph diversity trends throughout the Paleocene are not yet fully understood. More detailed and rigorous analyses of this record are therefore required, to accurately determine floral diversity patterns, and to shed light on their controlling processes.

CHAPTER 6: REGIONAL-SCALE SPATIAL HETEROGENEITY IN THE LATE PALEOCENE PARATROPICAL FORESTS OF THE U.S. GULF COAST

6.1 Introduction

Understanding how compositional heterogeneity in biotic assemblages varies through space is a primary goal for macroecologists. Studying spatial heterogeneity informs about community and meta-community assembly (Whittaker, 1960; Hubbell, 2001; Condit et al., 2002; Chase, 2010), the maintenance of regional species richness (Stevens, 1989; Rosenzweig, 1995; Qian et al., 2005, 2007), scale dependency of ecological processes (Soininen et al., 2007), and the sampling of biotic assemblages in both space and time (Nekola and White, 1999; White et al., 2010). The fossil record provides an empirical record of both the deep-time maintenance of patterns observed in modern systems, and changes in the spatial structuring of communities in response to large-scale environmental and climatic reorganizations.

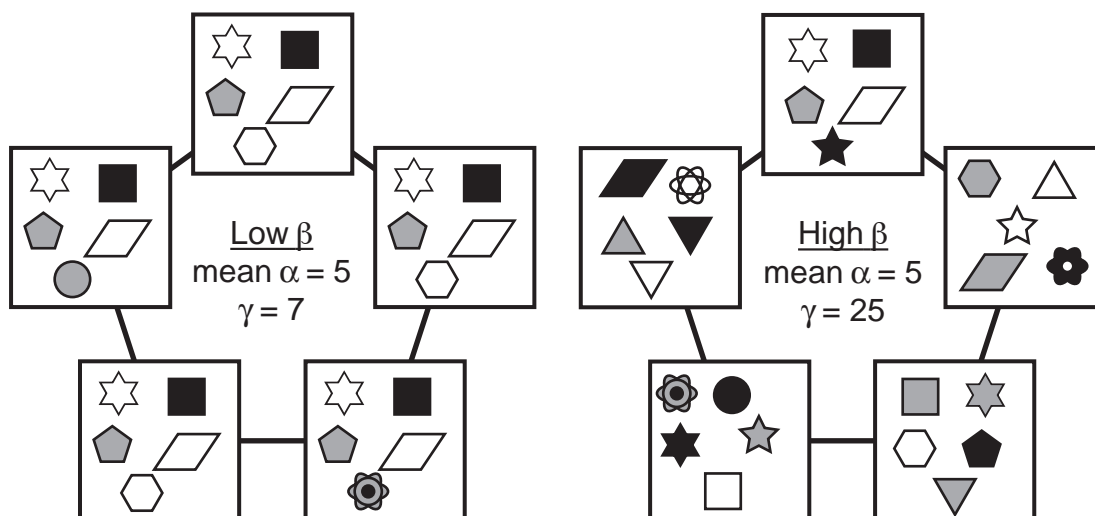
During the “greenhouse” phase of the early Palaeogene (Zachos et al., 2001, 2008) tropical climates extended into modern extra-tropical areas (Wilf et al., 2003; Fine and Ree, 2006; Jaramillo et al., 2006; Jablonski, 2008), and broad bands of “paratropical” forests covered much of the midlatitudes (Fine and Ree, 2006). To date there is little information on whether plant communities in these areas spatially resembled modern tropical or extra-tropical biomes. This is significant because it provides information on the relative importance of the regional climatic regime in determining spatial floral patterns. Given similar levels of environmental heterogeneity along a latitudinal gradient, it is expected that spatial heterogeneity

will increase with decreasing latitude, due to more equable climates facilitating greater habitat specialization towards the Tropics (Stevens, 1989). This pattern has been demonstrated for vascular plants and mammals in North America (Rodriguez and Arita, 2004; Qian and Ricklefs, 2007; Qian et al., 2009), although direct comparisons with tropical latitudes are currently lacking.

The GCP was part of the expanded tropical climatic zone during the early Palaeogene. Leaf morphologies, from which megathermal climatic estimates have been derived (Wolfe, 1978; Wolfe and Dilcher, 2000), testify to tropically functional plant types, whereas previous sporomorph studies have shown that taxonomically the vegetation was a mix of modern temperate and tropical lineages (Harrington, 2001; Harrington et al., 2004; Jardine and Harrington, 2008). The lack of a land bridge between North and South America limited compositional similarity between the GCP and Neotropics to ~0.7% in the late Paleocene (Jaramillo and Dilcher, 2001; Harrington and Jaramillo, 2007). Therefore, the spatial dynamics of the GCP paratropics were not simply “inherited” from range expansions from the tropical biome. The late Paleocene GCP sporomorph record is thus ideal for measuring spatial heterogeneity in an extra-tropical, megathermal setting.

Terms used to describe compositional heterogeneity through space have varied greatly among authors (Vellend, 2001; Magurran, 2004). Beta diversity and spatial turnover have commonly been used interchangeably, but here I follow Vellend (2001) in differentiating between them. In this scheme beta diversity is simply heterogeneity within a group of samples. Although my main interest here is in spatial heterogeneity (Fig. 6.1A), this can also relate to samples distributed

A) Low versus high β diversity



B) Low versus high spatial turnover

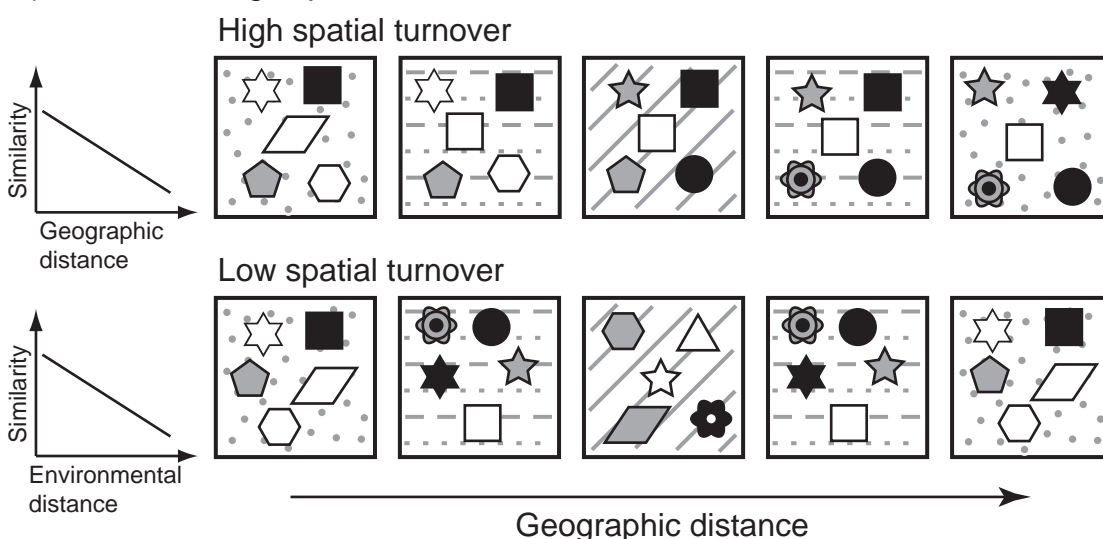


Figure 6.1. β diversity (among-sample heterogeneity) and spatial turnover in ecological systems. Large squares represent samples distributed in space; symbols represent different taxa found in those samples. α (within-sample) richness is held constant at $\alpha = 5$ throughout. A, Left group: many taxa are shared between samples, suppressing both β and γ (total) richness. Right group: no taxa are shared between samples, increasing both β and γ richness. B, The distribution of taxa along a geographic gradient. Background fill within squares represents environmental conditions, e.g., soil type or climate. Upper row: compositional similarity declines with geographic distance, regardless of the environmental characteristics of each sample. Lower row: within-sample composition is determined entirely by environmental variables, and compositional similarity declines with environmental, rather than geographic, distance.

temporally or environmentally. Note that beta diversity is not intrinsically tied to any specific spatial scale, such as habitat or local area (Gering et al., 2003), making its use more flexible across different sampling schemes. Turnover is defined as compositional change along a gradient. Spatial turnover therefore refers to compositional heterogeneity along a geographic gradient (Fig. 6.1B). As with beta diversity this is not bound to any specific spatial scale; thus the “geodispersity” concept of Miller et al. (2009) is simply spatial turnover writ large. Where there is a strong environmental control on species membership (as predicted by niche-assembly theories of spatial heterogeneity [Chave, 2008]; see Fig. 6.1B, lower row), beta diversity may be high but spatial turnover low.

In this chapter I use the late Paleocene GCP sporomorph record to explore spatial heterogeneity in megathermal, extra-tropical floras. I address two principal questions. First, how important was spatial heterogeneity for structuring the GCP palynoflora during the Paleocene? Second, how did the spatial structure of the GCP paratropical vegetation relate to modern tropical and extra-tropical biomes? I address this second question by using Holocene sporomorph data as a proxy record for modern plant communities.

I demonstrate that there are significant compositional differences geographically and between lithologies (clastic samples versus lignites) even though many taxa have widespread geographic distributions and occur in repeated associations across samples and formations. These data do not allow one to associate the Paleocene GCP more closely with either modern tropical or extra-tropical biomes. These results demonstrate the importance of spatial scale in determining spatial

patterns, and support an increased level of compositional heterogeneity in the modern Tropics compared to the extra-tropics.

6.2 Sampling spatial patterns in the fossil sporomorph record

A variety of biases can confound studies of spatial patterns in the fossil record. Here, I briefly discuss those that are relevant to the sporomorph record. The spatial area represented by a sample, termed “grain size” in the ecological literature (Nekola and White, 1999), will influence the patterns described. Larger grain sizes are expected to reduce the rate of spatial turnover between samples (Vellend, 2001; Mac Nally et al., 2004; Qian et al., 2005). Furthermore, species-area relationships dictate that, all else being equal, a smaller area will contain fewer species than a larger area (Rosenzweig, 1995; Nekola and White, 1999). Studies of spatial heterogeneity must therefore comprise samples of a similar grain size.

Fossil deposits frequently contain allochthonous components (individuals derived from outside of the sampling area [Kidwell and Holland, 2002]). The spatial grain of the sample is therefore larger than the actual sampled area, and how large depends on the source area for the deposit. The majority of the GCP sedimentary succession represents an estuarine to marginal marine depositional setting, with pollen derived from a regional to potentially sub-continental source area (Heusser, 1988; Haberle and Maslin, 1999; Colinvaux and De Oliveira, 2001; Harrington, 2001). Peat swamps, preserved as lignite deposits, typically contain para-autochthonous pollen types, derived predominantly from plants growing within and immediately around the swamp itself (Anderson and Muller, 1975; Jacobson and Bradshaw,

1981; Nichols and Pocknall, 1994; Nichols, 1995). It is therefore possible to study compositional patterns at both regional and local spatial scales simultaneously (see also Chapter 5).

As with spatial grain size, time-averaging (the amount of time represented by a sample) will influence the spatial pattern represented in a data set (White et al., 2010). Increasing the amount of time represented by a sample concomitantly increases the spatial area represented, by including more taxa that are only occasionally present in the sampled area and therefore missed in shorter sampling intervals (Magurran and Henderson, 2003; White et al., 2010). It is thus necessary to ensure that temporal sampling is similar among samples being compared. It is also essential that spatial comparisons be between coeval deposits, so that differences are due to compositional changes through space rather than through time.

Finally, the taxonomic rank used will influence the observed patterns. Supra-specific taxa are more geographically widespread than individual species, resulting in lower levels of spatial heterogeneity among samples (Qian and Ricklefs, 2007). Sporomorphs typically allow identification only to generic or familial level at best (Traverse, 1988). However, Qian and Ricklefs (2007) demonstrated that the latitudinal gradient in spatial turnover is still detectable at these taxonomic levels, albeit in a suppressed form compared to species-level comparisons. Thus there is no reason that low levels of taxonomic resolution imposed by the fossil sporomorph record (Traverse, 1988; Mander et al., 2010) should preclude its use for studying spatial patterns in plant assemblages.

6.3 Materials

The dataset used in this chapter comprises 28 samples from the Calvert Bluff Formation in Texas (representing the western GCP), and 28 samples from the Tuscahoma Formation in Mississippi and Alabama (the eastern GCP). Geological information concerning these formations is provided in Chapter 2, and locality and sampling information, and sedimentary logs, are provided in Chapter 3 (see Figs. 3.1 and 3.2). The Calvert Bluff Formation was sampled at five localities in east-central and east Texas: U.S. Silica Mine near Kosse, Walnut Creek Mining Company Calvert Mine near Bremond, Bastrop Golf Course in Bastrop, Red Bluff on the Colorado River in Bastrop, and a road cut eight miles north of Mt. Enterprise (Fig. 6.2). Most of the Tuscahoma Formation samples are from the OSM #2 Wahalak core. The Tuscahoma Formation in the Wahalak core is 154 m thick. Sporomorph yields were excellent throughout most of the formation, and sample coverage is much more complete than for the Calvert Bluff Formation. Two additional lignite samples from the very base of the Tuscahoma Formation were added from Red Hills Mine in Ackerman, Mississippi (see Chapter 5 and Fig. 6.2). These were included to provide a more similar sampling strategy for each study area, with lignite samples occurring at the top and bottom of each formation. This distribution ensures that temporal changes between lignite samples within each formation can be accounted for when assessing spatial differences between formations.

The sedimentary successions on each side of the GCP are highly similar (see Chapter 2), and are therefore a good comparison with which to explore spatial trends. Both the Calvert Bluff and Tuscahoma formations represent coastal plain

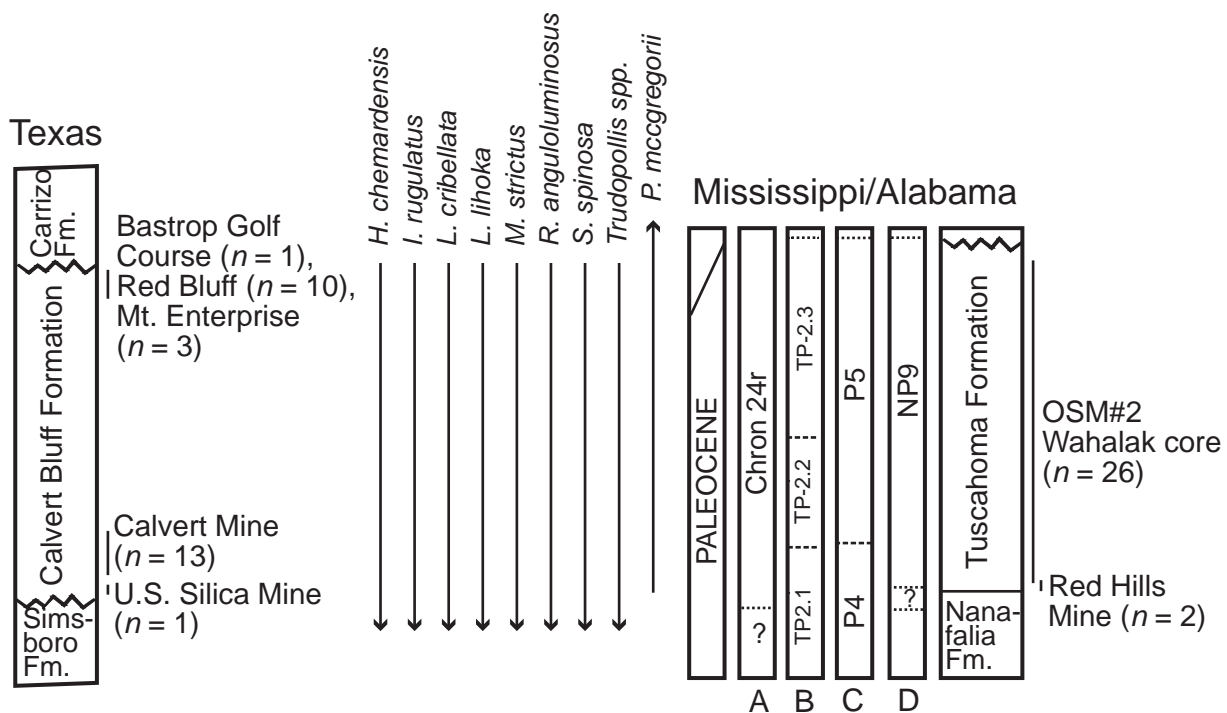


Figure 6.2. Sampling coverage for data used in this chapter, for Texas (left) and Mississippi/Alabama (right) (see also Chapter 3). Vertical lines next to stratigraphic sections indicate sample coverage for each locality; parentheses indicate number of samples from each locality. Taxon ranges are for biostratigraphic marker taxa from the latest Paleocene of Mississippi and Alabama that are also present in the Calvert Bluff Formation of Texas (see “Age Model” for discussion). Mississippi/Alabama stratigraphy adapted from Harrington and Jaramillo (2007): A, magnetostratigraphy (Rhodes et al., 1999); B, sequence stratigraphy (Mancini and Tew, 1991); C, planktonic foraminifera biozones (Mancini and Oliver, 1981; Berggren et al., 1995); D, calcareous nannoplankton biozones (Gibson et al., 1982) (see also Chapter 2).

sedimentation in a delta-dominated sedimentary system. Samples on the eastern Gulf Coast are representative of marginal marine to deltaic to emergent swamp environments (Mancini and Tew, 1991, 1995). Following the depositional model of Fisher and McGowen (1967), all localities sampled in the Calvert Bluff Formation represent fluvial-deltaic sedimentation, with associated swamp development. According to this model, the Bastrop Golf Course and Red Bluff sections may be more distal than the Silica Mine, Calvert Mine, and Mt. Enterprise sections. Dinoflagellates found in the Calvert Mine and Bastrop Golf Course samples demonstrate some level of marine influence.

A total of 139 morphospecies and 19,430 specimens were recorded from the 56 samples. Table 6.1 provides summary statistics for all of the samples analyzed. The widely used Chao2 species richness estimator (Colwell and Coddington, 1994) gave a richness estimate of $153.9 \text{ taxa} \pm 15.3$ (95% confidence interval) for the whole data set, which suggests that the data are not severely undersampled. Prior to data analysis all taxa that occur only in one sample were discarded from the data set. This led to the removal of 25 taxa, 21 of which were represented by only one specimen. This procedure ensures that compositional dissimilarities are not artificially inflated by differing sampling intensities (Foote and Raup, 1996; Olszewski and Patzkowsky, 2001a) and removes noise from the data set (Jaramillo, 2002).

6.4 Age model

The Paleogene sedimentary succession on the eastern GCP is well known through magnetostratigraphy (Rhodes et al., 1999), sequence stratigraphy (Mancini

Table 6.1. Sample details. Sample level = height from base of section for Calvert Bluff Formation samples, and core depth for OSM#2 Wahalak core (Tusahoma Formation) samples; N = sample count; S = raw within-sample species richness; R_{150} = rarefied within-sample species richness, at 150 grains per sample. See also Figure 3.2 for the position of samples on sedimentary logs for each core/locality.

Sample	Sample level (m)	Formation	Lithology	N	S	R_{150}
NAC/08/003	-	Calvert Bluff	Lignite	434	45	27.69
NAC/08/002	-	Calvert Bluff	Lignite	313	34	26.84
NAC/08/001	-	Calvert Bluff	Lignite	196	33	30.50
UCB/08/012	5.60	Calvert Bluff	Clastic	227	33	28.12
UCB/08/011	5.00	Calvert Bluff	Clastic	279	41	31.42
UCB/08/010	4.50	Calvert Bluff	Clastic	331	47	32.95
UCB/08/009	4.00	Calvert Bluff	Clastic	316	44	32.94
UCB/08/008	3.50	Calvert Bluff	Clastic	348	42	30.11
UCB/08/007	3.00	Calvert Bluff	Clastic	411	43	28.04
UCB/08/006	2.50	Calvert Bluff	Clastic	434	44	27.89
UCB/08/005	2.00	Calvert Bluff	Clastic	244	46	37.91
UCB/08/002	0.50	Calvert Bluff	Clastic	382	48	33.40
UCB/08/001	0.00	Calvert Bluff	Clastic	190	32	28.71
BGC/08/001	-	Calvert Bluff	Clastic	354	49	32.83
WCM/08/032	36.55	Calvert Bluff	Clastic	306	47	34.82
WCM/08/031	36.25	Calvert Bluff	Clastic	199	38	33.97
WCM/08/030	36.05	Calvert Bluff	Lignite	312	29	21.71
WCM/08/027	35.00	Calvert Bluff	Clastic	319	42	32.06
WCM/08/025	33.95	Calvert Bluff	Clastic	287	43	32.53
WCM/08/024	32.35	Calvert Bluff	Clastic	321	49	34.13
WCM/08/023	31.35	Calvert Bluff	Clastic	302	44	31.95
WCM/08/022	26.35	Calvert Bluff	Clastic	310	47	34.43
WCM/08/020	22.10	Calvert Bluff	Clastic	206	43	36.98
WCM/08/016	17.40	Calvert Bluff	Clastic	359	42	29.96
WCM/08/014	11.10	Calvert Bluff	Clastic	321	41	28.99
WCM/08/012	8.95	Calvert Bluff	Lignite	349	29	22.08
WCM/08/010	8.45	Calvert Bluff	Clastic	153	36	35.67
SM/08/001	-	Calvert Bluff	Lignite	373	33	25.24
WAH/08/061	76.50	Tusahoma	Lignite	623	21	13.61
WAH/08/060	77.42	Tusahoma	Lignite	319	35	26.51
WAH/08/059	81.63	Tusahoma	Clastic	458	44	25.76
WAH/08/057	87.78	Tusahoma	Clastic	795	38	18.71
WAH/08/054	91.64	Tusahoma	Lignite	301	40	31.85
WAH/08/052	97.84	Tusahoma	Clastic	313	32	24.50
GH08/Wa/051	101.35	Tusahoma	Clastic	396	45	27.94

Sample	Sample level (m)	Formation	Lithology	N	S	R ₁₅₀
GH08/Wa/048	106.07	Tuscahoma	Clastic	316	38	27.42
GH08/Wa/046	112.47	Tuscahoma	Clastic	309	45	32.35
GH08/Wa/043	119.30	Tuscahoma	Clastic	281	28	21.36
GH08/Wa/041	123.67	Tuscahoma	Clastic	334	40	26.87
GH08/Wa/038	128.37	Tuscahoma	Clastic	233	31	26.13
GH08/Wa/036	133.50	Tuscahoma	Clastic	322	35	24.48
GH08/Wa/034	136.96	Tuscahoma	Clastic	308	49	31.70
WAH/08/047	156.74	Tuscahoma	Clastic	287	55	41.82
WAH/08/044	162.36	Tuscahoma	Clastic	311	36	28.01
WAH/08/043	165.86	Tuscahoma	Clastic	472	42	27.04
WAH/08/038	172.57	Tuscahoma	Clastic	314	49	34.54
WAH/08/037	175.85	Tuscahoma	Clastic	389	40	26.17
WAH/08/036	180.52	Tuscahoma	Clastic	307	46	33.65
WAH/08/032	187.99	Tuscahoma	Clastic	309	44	32.56
WAH/08/026	197.18	Tuscahoma	Clastic	233	36	29.36
WAH/08/023	202.08	Tuscahoma	Clastic	307	43	32.52
GH08/Wa/028	208.94	Tuscahoma	Clastic	347	44	29.25
GH08/Wa/027	211.33	Tuscahoma	Clastic	331	33	24.24
GH08/Wa/024	216.84	Tuscahoma	Clastic	269	44	32.01
GH00/AC/012	-	Tuscahoma	Lignite	302	35	26.04
GH00/AC/009	-	Tuscahoma	Lignite	1368	30	13.20

and Tew, 1995), planktonic foraminifera (Mancini and Oliver, 1981; Mancini, 1984; Berggren et al., 1985), calcareous nannoplankton (Gibson et al., 1982) and pollen (Frederiksen 1980a, 1988, 1991, 1998; Harrington 2001, 2003b, 2008). The late Paleocene–early Eocene succession on the western GCP is much more poorly dated, because calcareous microfossils are lacking from these sediments in Texas (Loeblich and Tappan 1957), and to date no magnetostratigraphic work has been published.

Using sporomorphs from across the U.S. Gulf Coast, Fairchild and Elsik (1969) broadly correlated the Tuscahoma Formation of Mississippi and Alabama with the Rockdale Formation (now regarded as the Calvert Bluff Formation and the underlying Simsboro and Hooper Formations [Elsik, 1978]) of Texas. I have used

biostratigraphically important sporomorph taxa within my samples to confirm and refine this correlation.

Fourteen samples taken from the three localities at the very top of the Calvert Bluff Formation yielded no diagnostic Eocene taxa known from the uppermost part of the Tusahoma Formation (e.g. *Brosipollis* spp., *Celtis tschudyi*, *Granulatisporites luteticus*, *Interpollis microsupplingensis*, *Nuxpollenites* spp., *Platycarya* spp., *Retistephanocolporites* sp., *Symplocos?* *contracta* and *Thompsonipollis sabinetownensis* [Tschudy, 1973a; Frederiksen, 1998; Harrington, 2003b; Harrington et al., 2004; Harrington and Jaramillo, 2007]); only Paleocene marker taxa were recorded (*Holkopollenites chemardensis*, *Insulapollenites rugulatus*, *Lanagiopollis cribellata*, *Lanagiopollis lihoka*, *Momipites strictus*, *Retitrescolpites anguloluminosus*, *Spinaepollis spinosa* and *Trudopollis* spp. [Frederiksen, 1998; Harrington, 2008]). This concurs with Crabaugh and Elsik (2000) and Elsik and Crabaugh (2001), who placed the first appearance of *Platycarya* spp. at the contact between the Calvert Bluff Formation and the overlying Sabinetown Formation. From the localities that I have studied, I therefore consider the Calvert Bluff Formation to be entirely late Paleocene in age.

Only a few sparsely represented pollen taxa can be used to differentiate the Tusahoma Formation from the underlying Nanafalia Formation (Frederiksen, 1998). *Pistillipollenites mcgregorii* first appears at the base of the Tusahoma Formation (Frederiksen, 1998), and this is present in samples from the base and top of the Calvert Bluff Formation. Furthermore, Dickey and Yancey (2010) recovered *Bagelopollis verrucatus*, which first appears in the middle of the Tusahoma Formation (Frederiksen, 1998), from the Red Bluff locality at Bastrop (uppermost Calvert

Bluff), along with the Paleocene marker taxon *Spinaepollis spinosa*. The illustrated *Platycarya* of Dickey and Yancey (2010) is atypical of the form genus and not representative of the classical form that is found in the early Eocene. The Paleocene part of the Tuscaloosa Formation and the Calvert Bluff Formation are thus treated as being laterally equivalent and broadly coeval, with both formations representing approximately 1 Myr of the latest Paleocene.

6.5 The biogeographic structure of the Paleocene GCP palynoflora

6.5.1 Methods

I have used additive diversity partitioning (Lande, 1996) to assess the distribution of diversity within and between samples and formations, and two exploratory multivariate techniques, ordination and cluster analysis, to identify compositional patterns and taxonomic associations within the data set. Both ordination and cluster analysis can be used with abundance or incidence data. Although I have abundance information in the form of sporomorph sample counts, I have limited the following analyses to incidence data. Sporomorphs vary in their transportation potential because of differences in size, shape, and density (Heusser, 1988; Holmes, 1994). Sorting by water flow therefore may bias the relative abundances of sporomorph taxa differently in each formation, given some level of environmental variation across the GCP. Furthermore, ordinations and cluster analyses carried out with abundance data also gave results highly similar to those based on incidence data. I used the Jaccard similarity coefficient for these analyses because this metric is considered to perform well in ecological studies (Shi, 1993;

Legendre and Legendre, 1998).

I have correlated the Calvert Bluff and Tuscaloosa formations by using biostratigraphically important sporomorph taxa. Using these same taxa to assess compositional similarity between formations may bias the results by introducing circularity. Arguably, however, these taxa were a part of the GCP flora, and excluding them from comparisons would be expected to increase the differentiation between the two formations, increasing the chances of a Type 1 statistical error (i.e., spuriously finding a significant difference [Hammer and Harper, 2006]). Repeating the analyses with the biostratigraphic taxa removed did not alter the results; therefore I present findings for the full data set, with biostratigraphic taxa included.

Additive Diversity Partitioning

Lande (1996) reintroduced additive diversity partitioning (ADP) to the ecological literature as a means of measuring within- and among-sample diversity as proportions of the total diversity of a set of samples. Wagner et al. (2000) extended this approach to encompass multiple sampling scales. ADP has been used in many ecological (DeVries et al., 1997, 1999; Wagner et al., 2000; Gering et al., 2003; Summerville et al., 2003a,b; Summerville and Crist, 2005; Veech and Crist, 2007) and, more recently, palaeoecological (Layou, 2007; Patzkowsky and Holland, 2007; Heim, 2009; Holland, 2010; Mander et al., 2010) applications. Here, I use ADP in association with randomization procedures to study diversity and compositional heterogeneity within and between samples and formations.

ADP decomposes the total diversity (richness or an appropriate measure of

evenness) of a set of samples into α and β components using the general formula $\gamma = \alpha + \beta$ (Lande, 1996). The β component can easily be calculated by rearranging this equation, so that $\beta = \gamma - \alpha$. This treatment of β diversity has the attractive property of using the same unit of measurement for α , β , and γ diversity (Crist et al., 2003). Therefore γ is the total diversity of the pooled set of samples, α is the mean within sample diversity, and β is the mean among sample diversity, or the average diversity not found in any one sample (Veech et al., 2002). Applying ADP to the scenarios in Figure 6.1A gives $\alpha = 5$, $\beta = 2$ and $\gamma = 7$ for the left-hand set of samples (“Low β ”), and $\alpha = 5$, $\beta = 20$, and $\gamma = 25$ for the right-hand set of samples (“High β ”).

Where the sampling scheme is nested and hierarchical, the additive approach can be extended to take into account ever increasing scales of sampling (Wagner et al., 2000). In this study, samples (sampling level one) are nested within formations (sampling level two), which are nested within the total “regional” sampling scale γ (Fig. 6.3). Thus $\gamma = \alpha_{2(\text{formation})} + \beta_{2(\text{formation})}$, and $\alpha_{2(\text{formation})} = \alpha_{1(\text{sample})} + \beta_{1(\text{sample})}$. By substitution, $\gamma = \alpha_{1(\text{sample})} + \beta_{1(\text{sample})} + \beta_{2(\text{formation})}$. It is therefore possible to describe which sampling level contributes most to total diversity. Given my operational definition of β diversity as the heterogeneity within a group of samples, ADP is the ideal tool to quantify it in a complex, nested sampling design.

Rather than using individual-based rarefaction (Gotelli and Colwell, 2001), ADP corrects for varying sample sizes by using a weighting factor in obtaining mean α diversity. The mean α diversity of j samples at each hierarchical level i is obtained by $\alpha_i = \sum D_{ij} q_{ij}$, where D_{ij} is the diversity of each sample, and q_{ij} are the sample weights calculated by the proportion of the total number of individuals in level i that are

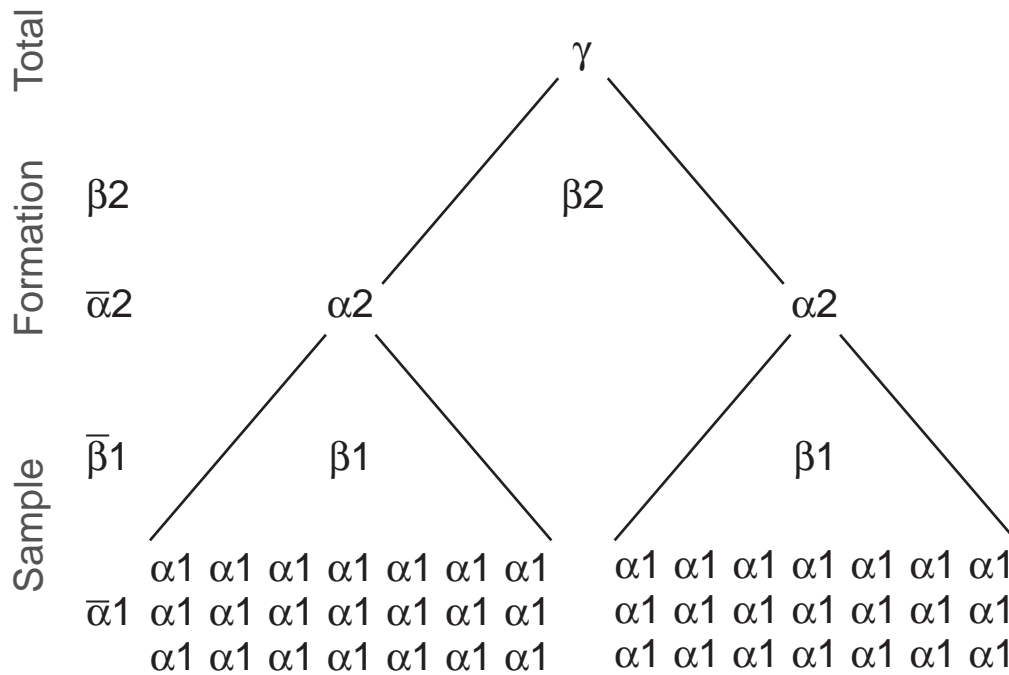


Figure 6.3. Sampling scheme used in this study. α = within-sampling-unit diversity, β = between-sampling-unit diversity, γ = total diversity. See text for details. Adapted from Patzkowsky and Holland (2007).

found in each sample j (Crist et al., 2003). Larger samples are therefore given more weight, under the assumption that they provide a more reliable estimate of diversity (Layou, 2007).

Crist et al. (2003) increased the explanatory power of ADP by developing a statistical framework for hypothesis testing. Crist et al. (2003) used randomization procedures to test for departures from random chance, by randomizing either individuals or samples. I have used the individual-based approach to test the hypothesis that the observed diversity partitioning could have been explained by a random distribution of individuals among samples at all hierarchical scales (Crist et al., 2003; Gering et al., 2003). I can then ask whether the between-formation (β_2)

level is larger than expected if individuals were randomly distributed in space (i.e., part of the same floristic assemblage). Therefore, this approach provides a test of whether composition is significantly different between the plant assemblages on the eastern and western GCP. If so, the within-formation (α_2) level must be smaller than expected by random chance, because in each sampling level $\gamma = \alpha + \beta$. This pattern is what we would expect given high levels of intra- and interspecific aggregation of individuals within the two formations. Additive partitioning combined with a null model has been used in various settings in the ecological and conservation biology literature (e.g. Crist et al., 2003; Gering et al., 2003; Summerville et al., 2003a,b, 2006; Veech and Crist, 2007); to my knowledge this is the first study to apply it to deep-time palaeoecology.

The randomization test works by shuffling individuals between samples, while preserving the original sample sizes and overall taxon abundances (Crist et al., 2003). Samples are then pooled into formations, and the randomized data set is partitioned into alpha and beta components, using the same procedure as with the actual data. By repeating this process many times (9999 in the present case), the null distributions of α and β estimates for each sampling level are produced. Probabilities can then be attached to the observed (actual) partitions by assessing the proportion of null values that are greater or less than them (Crist et al., 2003; Gering et al., 2003). For example, if one in 9999 of the expected null diversity values is greater than or equal to the observed value, then there is a probability (p -value) of 0.0001 of obtaining an estimate the same or greater than the observed value by chance. In this case the result is highly significant, and the null hypothesis is rejected (Legendre et

al., 1994; Crist et al., 2003).

ADP can be carried out on any diversity measure that is concave, i.e., where γ is always equal to or greater than α (Lande, 1996). Such measures include species richness and the Simpson and Shannon dominance metrics. Here I have used species richness because I am interested in taxon co-occurrence patterns between samples and formations, which is most clearly tested by considering the average number of taxa present (or not present) in each sample and formation compared to the null model, rather than the evenness/dominance structures at each sampling level. The interpretability of relative abundance distributions, which are described by evenness metrics, is also not clear for sporomorph samples. Different pollen dispersal mechanisms (especially animal versus wind dispersal) greatly influence the quantity of pollen produced by different taxa (Jackson, 1994; Bush, 1995; Bush and Rivera, 2001), which likely will distort the true relative abundances of the parent plant species (Odgaard, 1999).

Sample Ordination

To further understand the compositional structure of the Paleocene GCP palynoflora, I have ordinated the samples using nonmetric multidimensional scaling (NMDS; see Chapter 5, section 5.3.3 for rationale and approach). Ordinations are powerful techniques for detecting compositional patterns and gradients in community data sets (Legendre and Legendre 1998), whereas ADP can only provide information on predefined groups of samples (formations in the present case). ADP also averages across samples at each level in the sampling hierarchy, and so it does

not inform about the relationships between individual samples.

Cluster Analysis

I have used agglomerative, hierarchical cluster analysis as a complement to NMDS, and to explore taxonomic associations across the GCP. Like ordination methods, cluster analysis is a multivariate technique that depicts structure within the data. Cluster analysis classifies samples (Q-mode) or species (R-mode) into groups based on the similarity of their compositions or associations respectively (Sneath and Sokal, 1973; Legendre and Legendre, 1998). By its nature hierarchical cluster analysis imposes a nested, hierarchical structure on the data whether one is present or not (Springer and Bambach, 1985); however, comparison with NMDS ensures that spurious groupings will not be misinterpreted.

I carried out a two-way cluster analysis (Springer and Bambach, 1985; Olszewski and Patzkowsky, 2001b), in which the dendrograms from both Q-mode and R-mode cluster analyses are used to reorder the rows and columns of the original samples by species matrix. This allows clusters of taxa to be related to clusters of samples, to better understand the taxonomic structure of sample groupings. I used the Unweighted Pair Group Method with Arithmetic Averaging (UPGMA) linkage algorithm (van Tongeren, 1995; Legendre and Legendre, 1998) to produce cluster dendrograms. The UPGMA linking algorithm is an intermediate between the single- and complete-linkage algorithms; it minimizes the artificial gradients imposed by the former and artificial discrete groupings imposed by the latter (van Tongeren, 1995).

6.5.2 Results

Additive Diversity Partitioning

When partitioning is carried out on all samples (Fig. 6.4), the observed data show that the largest partition is the within-formation (α_2) level ($=\alpha_{1(\text{sample})} + \beta_{1(\text{sample})}$), which makes up 90% of total richness. Partitioning this into α and β components shows the importance of the among-sample (β_1) level, which makes up 56% of the total richness. The between-formation (β_2) level is the smallest partition, constituting only 10% of the total. However, when compared to the expected partitioning produced by the randomization procedure, it can be seen that both the β_1 and β_2 levels are significantly larger than expected by chance ($p < 0.001$). Average within-sample (α_1) and within-formation (α_2) richness contribute significantly less to the total richness than would be expected by chance ($p < 0.001$). A significant compositional difference between formations is therefore supported, although among-sample heterogeneity is clearly important.

When partitioning is carried out on the lignite samples only (Fig. 6.4), the α_2 and β_2 levels are no longer significantly different from the null model. As with the analysis of the whole data set, observed α_1 richness contributes significantly less to the total richness than would be expected by chance ($p < 0.001$), and β_1 contributes significantly more ($p < 0.001$). Both α_1 and α_2 richness constitute proportionally more of the total richness in the lignite samples than in the whole data set (Fig. 6.4). Total richness is lower (55 taxa as opposed to 114 for all samples combined) because not all taxa occur in the 11 lignite samples.

The significant compositional difference between formations was confirmed

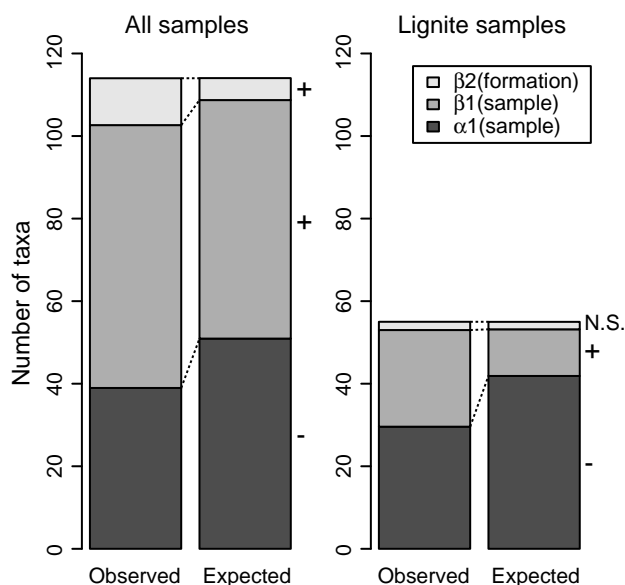


Figure 6.4. Additive partitioning of species richness for all samples (left) and lignite samples only (right). “Observed” refers to partitions for the actual data, and “Expected” to partitions derived from the randomization procedure (9999 randomizations). Plus sign indicates that the observed partition is significantly larger than expected ($p < 0.001$), and minus sign that it is significantly smaller than expected ($p < 0.001$). N.S. = not significant at $p = 0.05$. $\alpha_2(\text{formation}) = \alpha_1(\text{sample}) + \beta_1(\text{sample})$.

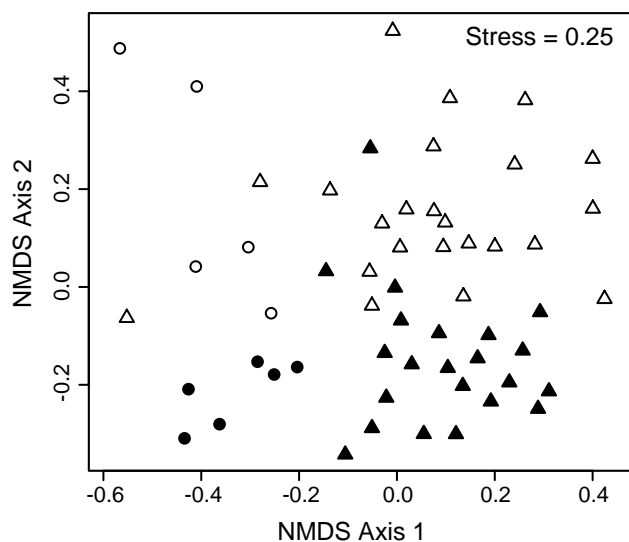


Figure 6.5. Nonmetric multidimensional scaling (NMDS) plots of GCP samples using incidence data and the Jaccard coefficient. Open symbols are Tuscahoma Formation samples, closed symbols are Calvert Bluff Formation samples, triangles are clastic samples, and circles are lignite samples.

with nonparametric multivariate analysis of variance (NPMANOVA) tests (Anderson, 2001). NPMANOVA is analogous to a traditional multivariate ANOVA, but being nonparametric, it makes no assumptions about multivariate normality (Anderson, 2001). I ran the tests on incidence data using the Jaccard similarity metric (Shi, 1993). Highly significant differences were found both for the whole data set ($F = 4.55$, $p = 0.001$) and, in contrast to the ADP analysis, for lignite samples only ($F = 1.74$, $p = 0.048$). This suggests that NPMANOVA may be more robust to smaller sample sizes, or lower between-group dissimilarities.

NMDS

When plotted (Fig. 6.5), the samples from the Tuscahoma (open data points) and Calvert Bluff (black data points) formations are well separated in ordination space, with only minimal overlap. Importantly, the lignite samples (circles) maintain this separation, demonstrating that they show the same overall pattern as the space-averaged marginal marine clastic samples. Whereas the samples from the two formations are separated along NMDS axis two, the lignite and clastic samples are separated along NMDS axis one. This demonstrates a clear lithological control on composition, with clastic samples having additional compositional inputs from outside the immediate area of the coastal swamps.

To explore fine-scale compositional patterns within the formations, we ran NMDS on each formation separately. When the samples from the Calvert Bluff Formation are ordinated (Fig. 6.6A), there is a clear distinction between the lignite (circles) and clastic (triangles) samples on NMDS axis 1. Clastic samples

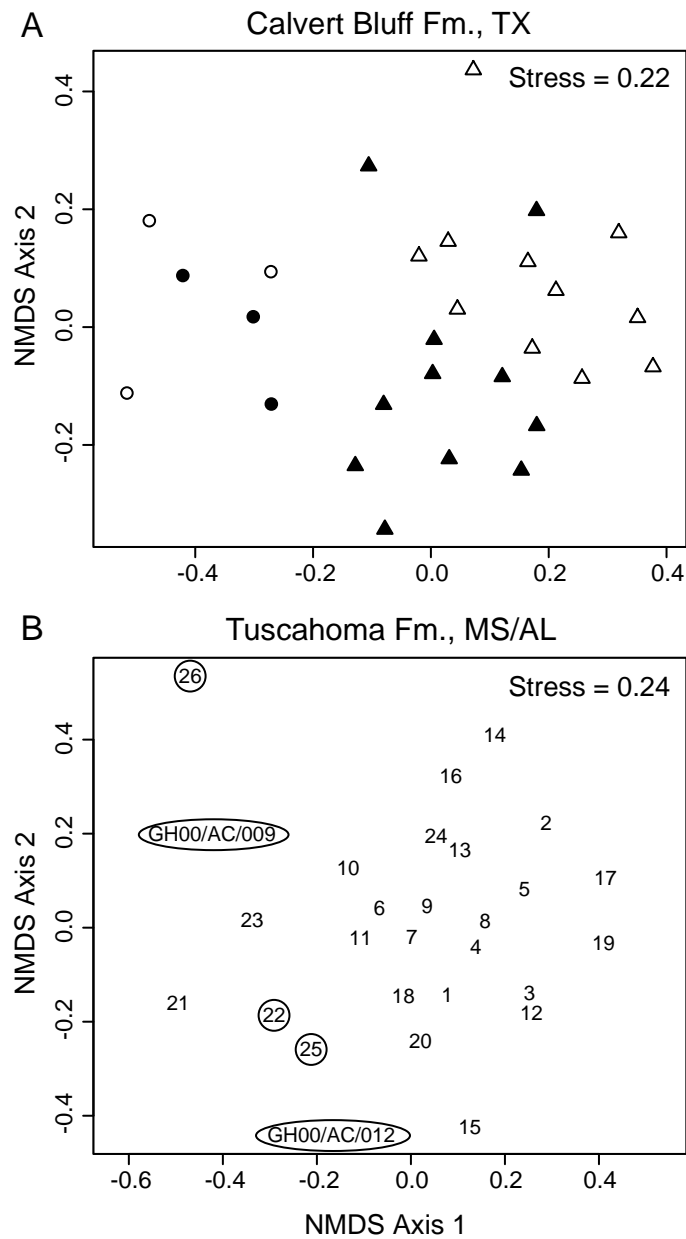


Figure 6.6. Nonmetric multidimensional scaling (NMDS) plots of each formation separately. A, Calvert Bluff Formation: open symbols indicate samples from the base of the formation, closed symbols indicate samples from the top of the formation, triangles indicate clastic samples, and circles indicate lignite samples. B, Tuscahoma Formation: numbers indicate sample level in OSM#2 Wahalak core (1 = base, 26 = top), Red Hills Mine samples are denoted by their sample number. Ringed numbers are lignite samples. Note the different axis scales on the two plots.

from the top (black symbols) and bottom (open symbols) of the formation occur in two overlapping clusters, whereas the lignite samples occur in one cluster. The Tuscahoma Formation (Fig. 6.6B) shows a general compositional separation between the clastic and lignite (circled) samples. As with the Calvert Bluff lignites there is no obvious separation temporally or spatially. The two clastic samples occurring close to the lignites occur immediately above and below a lignite seam in the OSM#2 Wahalak core. The remaining clastic samples from the OSM#2 Wahalak core do not show any obvious gradient or grouping through time.

Cluster analysis

Several main points can be drawn from the two-way cluster analysis (Fig. 6.7). Samples (the dendrogram to the left) form clusters based primarily on lithology: clastic samples occur mostly in clusters A to F, and lignite samples occur exclusively in clusters G and H. Clusters within these groups are dominated by one formation or the other, but there is no single break between Calvert Bluff and Tuscahoma samples. This is to be expected, given that the NMDS (Fig. 6.5) revealed some overlap between formations. Taxa (the upper dendrogram) form less clear clusters than the samples, with many taxa occurring individually rather than in groups. Because “chaining” is not a characteristic bias of the UPGMA algorithm (van Tongeren, 1995), this probably represents a genuine gradient in the data, reflecting an increase in the incidence of taxa among samples from cluster I to cluster VIII. Samples occupy a smaller range of similarity values (between 0.3 and 0.6) than do taxa (0.0 to 1.0).

Using both R- and Q-mode analyses to relate taxon associations to sample

clusters reveals that most taxa are not limited to one group of samples; instead associations of taxa are diffuse among samples, formations, and lithologies. This is unsurprising, given that 92 of the 114 taxa in the data set (=81%) are shared between the two formations. The most common ranked taxa (those that occur in multiple samples) are also largely the same in each formation (Fig. 6.8). Some relationships can be picked out from the two-way cluster analysis, however. Lignites (clusters G and H) are marked by the lack of taxa from cluster VI (e.g. *Cingulatisporites* spp., *Ericipites* spp., *Ulmipollenites krempii*, *Camaronosporites grootii*, *Momipites waltmanensis*, *Bombacacidites reticulatus*, *Caryapollenites wodehousei*; and the biostratigraphic marker taxa *Retitrescolpites anguloluminosus*, *Momipites strictus*, and *Pistillipollenites mcgregorii*) and by the presence of taxa from cluster V (e.g. *Aesculiidites circumstriatus*, *Momipites triradiatus*, *Caprifoliipites* spp., *Horniella* spp. and *Rhoipites* sp. 1). Cluster A contains mainly Calvert Bluff clastics and is separated by cluster II taxa (e.g. *Intratropipollenites pseudinstructus*, *Insulapollenites rugulatus*, *Spinizonocolpites prominatus*, *Sequoiapollenites* spp. and *Toroisporites* spp.); clusters B and E are delineated by cluster III taxa (e.g. *Ailanthipites berryi*; the Normapolles *Basopollis obscurocostatus*, *Trudopollis plenus*, and *Pseudoplicapollis limitatus*; and the spore *Zlivosporis novamexicanum*).

6.5.3 Compositional heterogeneity in the Paleocene GCP palynoflora

These results demonstrate that the flora across the GCP during the late Paleocene was not compositionally homogeneous. A separation between the Calvert Bluff Formation in Texas and the Tusahoma Formation in Mississippi and Alabama

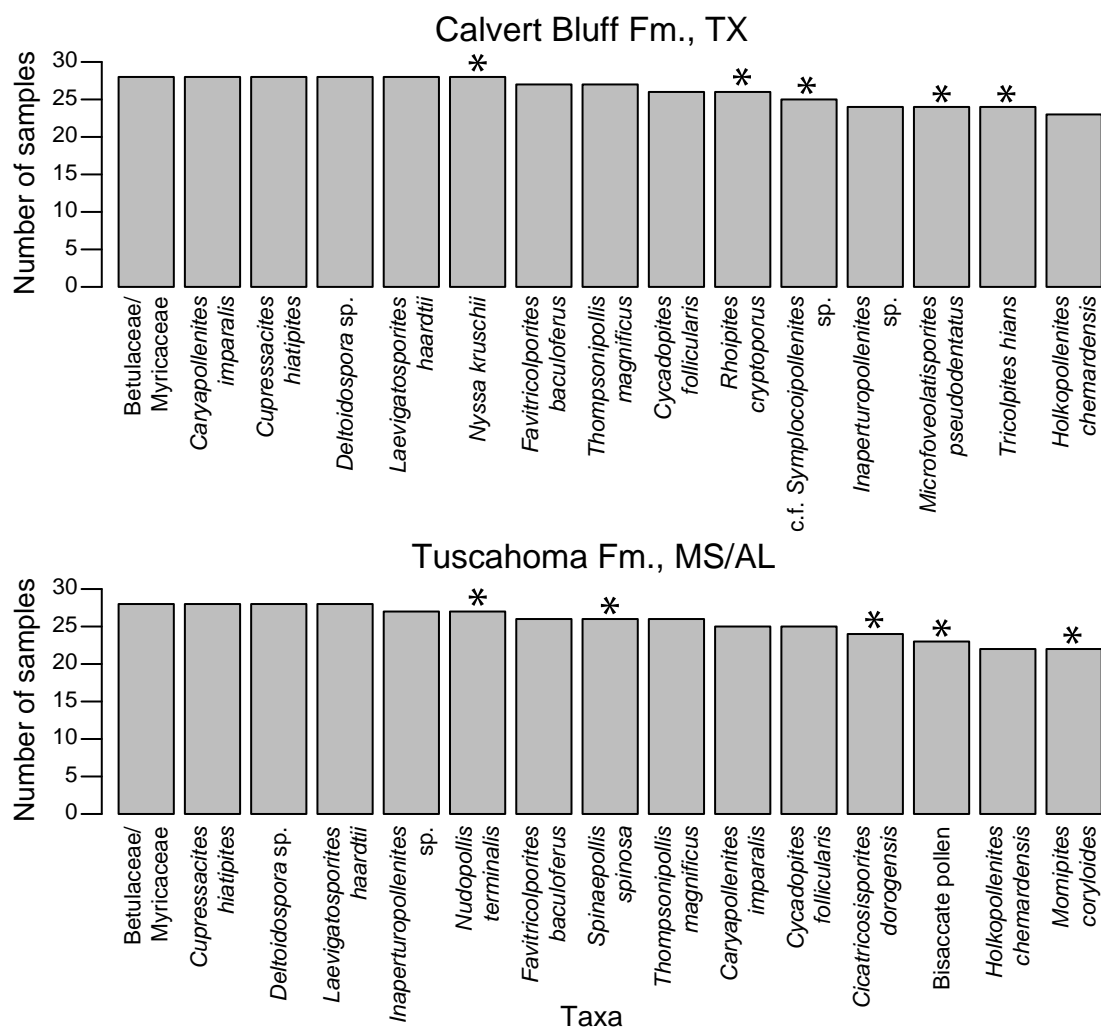


Figure 6.8. Incidence plots for the 15 most common taxa within each formation. The y-axis shows the number of samples in which each taxon occurs. Asterisks denote the taxa in each formation that are not among the 15 most common taxa in the other formation.

was demonstrated by the ADP analysis (when both clastic and lignite samples were used), NPMANOVA (when using the whole data set or with the lignite samples only), NMDS, and cluster analysis. Similar floral discontinuities on regional scales have been discovered in Amazonia and have been related to changes in soil characteristics and underlying geology (Pitman et al., 2008; Coronado et al., 2009; Duque et al., 2009). Ecological processes within the GCP floras can only be speculated upon, given the lack of knowledge of fine-scale environmental and habitat changes within this region and of the environmental tolerances of plant taxa (or even what the plant taxa are below family level). No geographic barrier to species interchange across the GCP is known, apart from the subsiding Mississippi embayment (Cox and Van Arsdale, 2002).

In the ~1-Myr time window of this study, compositional differentiation was mainly in the spatial dimension; compositional turnover through time was only of secondary importance in driving among-sample heterogeneity. NMDS showed some differentiation between clastic samples from the top and bottom of the Calvert Bluff Formation (Fig. 6.6), but this was less important than the differentiation between the two formations (Fig. 6.5). All lignite samples from the Calvert Bluff Formation plotted close together, demonstrating stability in these swamps through time and space (~200 km). The Tusahoma samples did not reveal any clear temporal trends (Fig. 6.6), although the differences in sampling distribution and intensity between the two formations may have influenced this. A general pattern of change over time has previously been recorded within the Tusahoma Formation (Harrington and Jaramillo, 2007), with samples taken from the base of the formation being

compositionally different from those at the top. The pattern of change on both western and eastern sides of the U.S. Gulf Coastal Plain can be attributed to the long-term climate warming in the late Paleocene evident from isotope and other climate proxy data (Wilf, 2000; Fricke and Wing, 2004; Zachos et al., 2008).

The most pervasive segregation observed in the multivariate analyses is lithological rather than spatial. Clastic and lignite samples clearly separate out in the NMDS and cluster analysis plots (Figs. 6.5–6.7), although no taxa are completely restricted to the swamp environments (Fig. 6.7). This lithological differentiation demonstrates the need to take taphonomic and environmental factors into account in spatial analyses. Lower within-sample richness in the lignites relative to the clastic samples, as demonstrated by the ADP analysis (Fig. 6.4), is a common feature of such deposits (Nichols and Traverse, 1971; Jaramillo et al., 2007; Harrington, 2008; see also Chapter 5). This may be caused by the restricted sporomorph source area for swamps relative to marginal marine and lacustrine settings (Nichols and Traverse, 1971), or the special adaptations needed by plant taxa to inhabit a swamp environment (Fitter and Hay, 2002). The clastic sediments sample both the local and regional vegetation (Harrington, 2008). The maintenance of the geographic separation between formations in the lignite samples, as demonstrated by NMDS and NPMANOVA, means those extra-local taxa are not biasing the signal displayed by the data set as a whole.

Despite the prevalence of compositional heterogeneity in this biome (both among samples and between formations), many common taxa are widespread across the GCP (Figs. 6.7 and 6.8). Taxonomic associations are diffuse and recur within and

between formations, which suggests a regional species pool arranged into repeated, co-occurring groups of taxa distributed across the GCP. Similar patterns have been recorded in both temperate (Nekola and White, 1999) and tropical (Pitman et al., 1999, 2001; Macia and Svenning, 2005; Pitman et al., 2008) forests in areas of low environmental heterogeneity.

6.6 Relating the Paleocene GCP to Holocene biomes

6.6.1 Methods

Holocene dataset details

To compare the spatial dynamics of the Paleocene GCP with modern biomes, I have used previously published Holocene lake core data. All data were taken either from the online Neotoma database (the new repository for the Global Pollen Database; <http://www.neotomadb.org/>), or from personal communications (Table 6.2 and Fig. 6.9). Tropical sites ($n = 5$) were taken from the Colombian and Brazilian Neotropics, close to the equator. Extra-tropical sites were taken from eastern North America, and were divided into warm mixed forest (25°N to 36°N; $n = 11$) and temperate deciduous forest (26°N to 45°N; $n = 11$). North American biome names and coverage were taken from Williams et al. (2000). The warm mixed forest (also called broadleaved evergreen forest by Williams et al. [2000]) includes the modern GCP vegetation. Sites were chosen so that each biome covers a similar area, and all are cores from lakes less than 600 m above sea level.

I selected pollen samples dating from 3000 to 3500 Ka as a suitable time interval for comparing spatial patterns between Holocene biomes, because this

Table 6.2. Sampling information for Holocene datasets. Map. loc. = number on Figure 6.9 maps (locations of Temperate and Warm mixed sites are illustrated on Figure 6.9A, locations of Tropical sites are illustrated on Figure 6.9B); Lat. = latitude; Long. = longitude; Alt. = altitude; Range size = size of age range used in years; N = number of samples; Mid. lat. = midpoint latitude for group of samples; Mid. long. = midpoint longitude for group of samples. References are included in the main reference list at the end of the thesis.

Temperate									
Site	Map loc.	Lat.	Long.	Alt.	Core age range	Range used	Range size	N	References
Quarles Pond	1	38	-79.07	500	0-12647	2981-3790	809	2	Craig 1969
Stages Pond	2	39.67	-82.94	212	64-3739	3063-3401	338	2	Snyder et al 1991
Crider's Pond	3	39.97	-77.55	290	0-15744	3340-3846	506	2	Watts 1979
Fudger Lake	4	40.1	-85.53	320	0-14596	3063-3602	539	3	Shane 1991; Shane and Anderson 1993
Silver Lake	5	40.35	-83.8	332	0-16000	3191-3518	327	2	Odgen 1966, 1969
Ladd Lake	6	41.41	-84.75	249	0-13673	3194-3484	290	2	Shane 1991; Shane and Anderson 1993
Pretty Lake	7	41.58	-85.25	294	0-13930	3251-3654	403	3	Odgen 1969; Williams 1974
Hudson Lake	8	41.67	-86.53	239	42-14116	3326-3621	295	3	Bailey 1972
Spring Lake	9	41.67	-76.35	342	0-13678	3217-3626	409	2	None given on Neotoma
Mohawk Pond	10	41.81	-73.28	360	200-15776	3068-3534	466	2	Gaudreau 1986
North Pond	11	42.65	-73.05	586	0-11327	3142-3506	364	2	Whitehead and Crisman 1978
Mean:							431		
Site combinations for spatial averaging regression						Mid. lat.	Mid. long.		
North Pond zone: North Pond and Mohawk Pond						42.23	-73.17		
Crider's Pond zone: Crider's Pond and Quarles Pond						38.99	-78.31		
Stages Pond zone: Stages Pond, Silver Lake and Fudger Lake						40.04	-84.09		
Ladd Lake zone: Ladd Lake, Pretty Lake and Hudson Lake						41.55	-85.51		

Warm mixed									
Site	Map loc.	Lat.	Long.	Alt.	Core age range	Range used	Range size	N	References
Buck Lake	12	27.23	-81.33	45	0-8544	2679-3336	657	2	None given on Neotoma
Scott Lake	13	27.97	-81.95	51	0-4527	3057-3324	267	2	Watts 1971
Mud Lake	14	29.3	-81.87	15	0-8859	2944-3476	523	2	Bradley 1966; Watts 1969, 1971
Camel Lake	15	30.27	-85.02	20	0-36658	3203-3695	492	3	Watts et al 1992
Langdale Pond	16	30.64	-83.20	58	0-8194	2851-3363	512	2	None given on Neotoma
Lake Louise D	17	30.73	-83.25	49	0-10641	3342-3830	488	2	Watts 1971
Goshen Springs	18	31.72	-86.13	105	0-54999	3506-3986	480	2	Delcourt 1980
Tombigbee	19	33.56	-88.47	49	0-10702	2831-3440	609	2	None given on Neotoma
Clear Pond	20	33.8	-78.95	10	0-20374	3237-3562	325	3	Hussey 1993
White Pond	21	34.17	-80.78	90	0-19386	3315-3848	533	2	Watts 1980
Anderson Pond	22	36.03	-85.5	305	0-24041	3391-3884	493	2	Delcourt 1979
Mean:							489		
Site combinations for spatial averaging regression						Mid. lat.	Mid. long.		
White Pond zone: White Pond and Clear Pond						33.99	-79.87		
Tombigbee zone: Tombigbee and Goshen Springs						32.64	-87.30		
Lake Louise zone: Lake Louise, Langdale Pond and Camel Lake						30.55	-83.82		
Mud Lake zone: Mud Lake, Scott Lake, and Buck Lake						28.17	-81.72		
Tropics									
Site	Map loc.	Lat.	Long.	Alt.	Core age range	Range used	Range size	N	References
Lagoa das Patas	23	0.27	-66.68	300	0-44569	3314-3867	553	2	Colinvaux et al 1996
Laguna Piusbi	24	1.88	-77.93	80	0-7670	3119-3338	219	4	Behling et al 1998; Behling pers. comm.
Laguna Mozambique	25	3.96	-73.05	175	0-3562	3169-3562	393	3	Berrio et al 2002; Berrio pers. comm.
Laguna Chenevo	26	4.08	-70.35	150	0-7260	3271-3573	302	2	Berrio et al 2002; Berrio pers. comm.
Laguna Jotaordó	27	5.8	-76.66	50	0-4230	4050-4230	180	8	Berrio et al 2000; Berrio pers. comm.
Mean:							329		

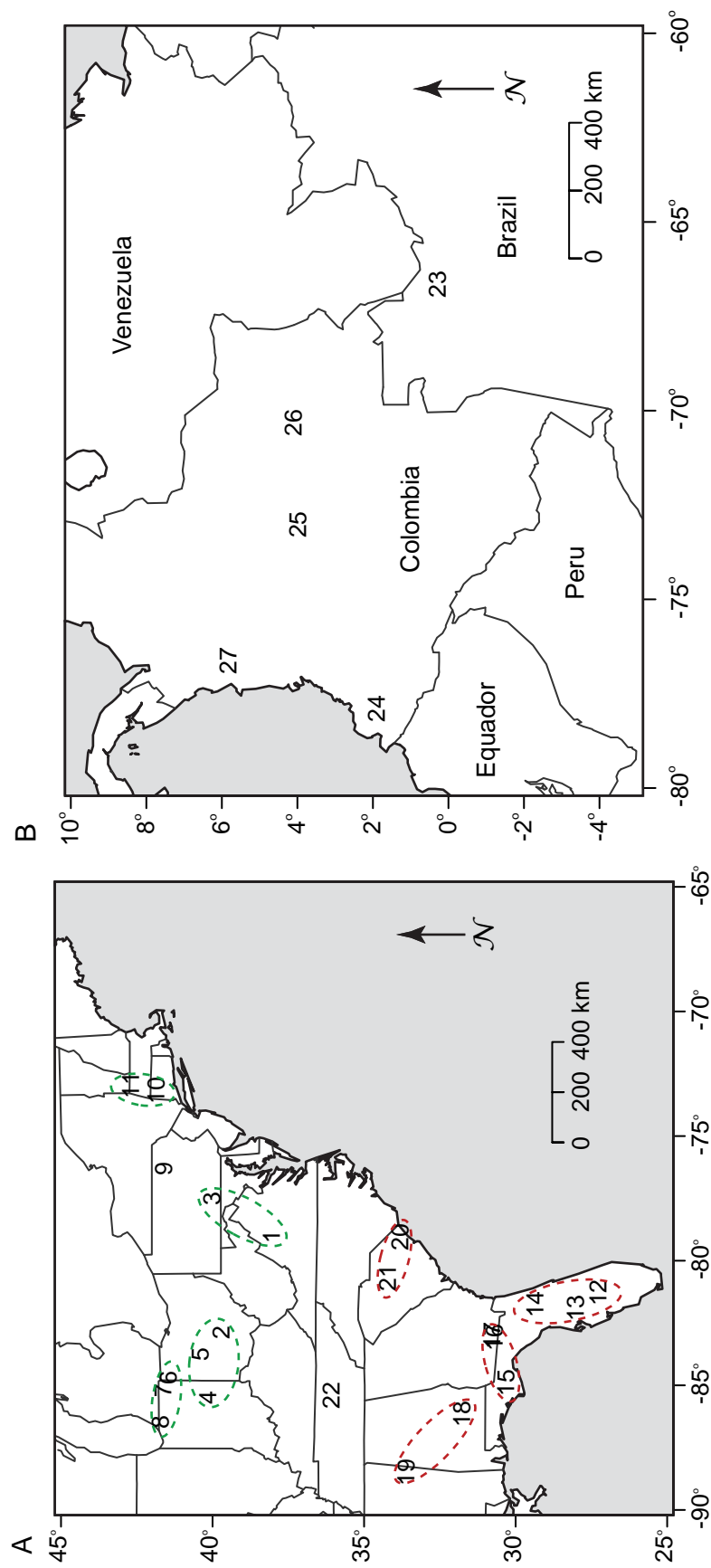


Figure 6.9. Locality maps for Holocene lakes. Numbers refer to localities in Table 6.2. A = North American localities (temperate and warm mixed biomes), B = South American localities (tropical biome). Dashed areas are zones used for spatial averaging regression; green = temperate, red = warm mixed.

post-dates the major climatic changes of the earlier Holocene and pre-dates major human alteration of the landscape (Mayle et al., 2000; Williams et al., 2000; Berrio et al., 2002; Munoz and Gajewski, 2010). Holocene pollen samples typically represent years to tens of years (Jacobson and Bradshaw, 1981); assuming a constant rate of sedimentation, samples from the OSM#2 Wahalak core represent 70-140 years (given a 1-Myr duration and 150 m of core for the Tuscahoma Formation, and 1-2 cm of core thickness per sample). Sedimentation rates were not uniform throughout deposition of the Tuscahoma Formation (Mancini and Tew, 1991, 1995), so time-averaging for the GCP data probably extends into several hundred years for some samples. To emulate this increased time-averaging in the Holocene data, two or three consecutive samples within each core were pooled. The Holocene samples used in this analysis therefore encompassed 200 to 700 years (Table 6.2).

Data Analysis

ADP is not appropriate for comparing the Paleocene and Holocene data because most of the Paleocene localities produced multiple samples arranged through time, leading to temporal pseudoreplication (Srivastava, 1999) in within- and between-sample comparisons that is not present in the Holocene data. I instead analyzed the distance decay of compositional similarity in the Holocene biomes, by regressing inter-site compositional similarities onto inter-site geographical distances (Nekola and White, 1999). A steeper slope demonstrates a more rapid decay of similarity with distance, and so a higher level of spatial turnover. Compositional similarity was measured as the natural logarithm of the Jaccard coefficient, which has

given the best linear fit in similar studies of modern ecological systems (Nekola and White, 1999). Geographic distance was measured as the great circle distance between sites, calculated using the R package “spdep,” version 0.4-7 (Bivand et al., 2007).

Using pairwise distances violates assumptions of independence in parametric linear regression (Legendre et al., 1994; Nekola and White, 1999). Because parametric p -values could therefore not be used, I used a permutation procedure, as outlined in Legendre et al. (1994), to assess the significance of the regressions. This procedure is analogous to the randomization test used with the ADP analyses (Crist et al., 2003). The response (compositional similarity) matrix is randomized, the regression performed, and the F -value stored (the R^2 -value can also be used, as F is a monotonically increasing function of R^2 [Legendre et al., 1994]). This procedure is repeated many times (9999 here), to create a distribution of null values under the expectation of random chance. The p -value is then the proportion of expected (permuted) F -values smaller than the observed F -value (i.e., the F -value from the original, unpermuted data).

The pervasive temporal pseudoreplication in the Paleocene GCP data prevented me from using linear regression as described above. Hence, I calculated the mean intersample compositional distance between the Calvert Bluff and Tuscaloosa formations, and compared this with the Holocene data by plotting it on the same distance-decay graphs, using 819 km as the geographic distance between sampling locality midpoints for each formation. Only clastic samples were used, to maintain isotaphonomic consistency. The intersample distances were not normally distributed (Shapiro-Wilk test of normality, $W = 0.98$, $p < 0.001$), so 95% confidence

intervals for the mean distance were calculated through a bootstrapping procedure. The inter-formation, intersample compositional similarities were resampled, with replacement, 10,000 times. The mean was calculated for each resampling run, and the 2.5% and 97.5% quantiles taken from this distribution.

Lake sediments are dominated by sporomorphs produced by vegetation in the surrounding tens to hundreds of meters, and maximum sporomorph source radii are typically on the order of tens of kilometers (Jacobson and Bradshaw, 1981; Sugita, 1993; Davis, 2000). The sporomorph source areas for the marginal marine samples of the Paleocene GCP are uncertain. However, given that the sedimentary systems on both sides of the GCP are associated with major deltaic complexes, and are therefore likely to have received significant fluvial sporomorph input, the source areas for these deposits are expected to be larger than for the Holocene lakes. As discussed above, increasing the duration of the sampling interval through artificial time-averaging is expected to increase the effective sampling area (White et al., 2010). To further investigate the effects of increased spatial grain on the distance-decay analysis, we pooled Holocene sites into zones with diameters of 300 km (see Table 6.2 and Fig. 6.9). This diameter was chosen as a trade-off between number of zones and number of sites/zone. Both temperate and warm mixed biomes were divided into four zones of two or three sites. This procedure was not carried out for the tropical biome, owing to the low number of sites. We then carried out regressions as described previously, using the great circle distance between zone midpoints.

6.6.2 Results

Regression of compositional similarity onto geographic distance (Table 6.3, Fig. 6.10A) reveals that the rate of spatial turnover in the Holocene tropical biome is greater than that of the two extra-tropical biomes. The tropical biome also has a higher intercept than the extra-tropical biomes. This means that geographically proximal sites are more similar in the Tropics than in extra-tropical biomes, up to the intersection of lines at ~900 km between sites. At greater distances between sites tropical floras are relatively less similar than extra-tropical ones.

When the regression is rerun with the spatially averaged temperate and warm mixed data sets (Fig. 6.10B), the warm mixed forests show both a steeper slope and a higher intercept than the temperate forests. Here the two regression lines cross at about 800 km between sites. As with the tropical versus extra-tropical biomes, this shows a higher rate of distance decay in the warm mixed forests, and scale dependency in relative compositional similarity between biomes. As expected, similarity values are higher for the spatially averaged (pooled sites) data set than for the individual sites regression.

The GCP data (the black cross in Fig. 6.10) plot out very close to the intersection point of the Holocene biome regression lines in the individual sites regression (Fig. 6.10A). Thus, given the distance between sampling localities in the Paleocene data and the spatial structure of the Holocene biomes, it is not possible to tell which biome the Paleocene GCP most closely resembles. Comparison with the spatially averaged data (Fig. 6.10B) shows that the GCP is more dissimilar than either the warm mixed or temperate biomes at this geographic distance. The GCP mean

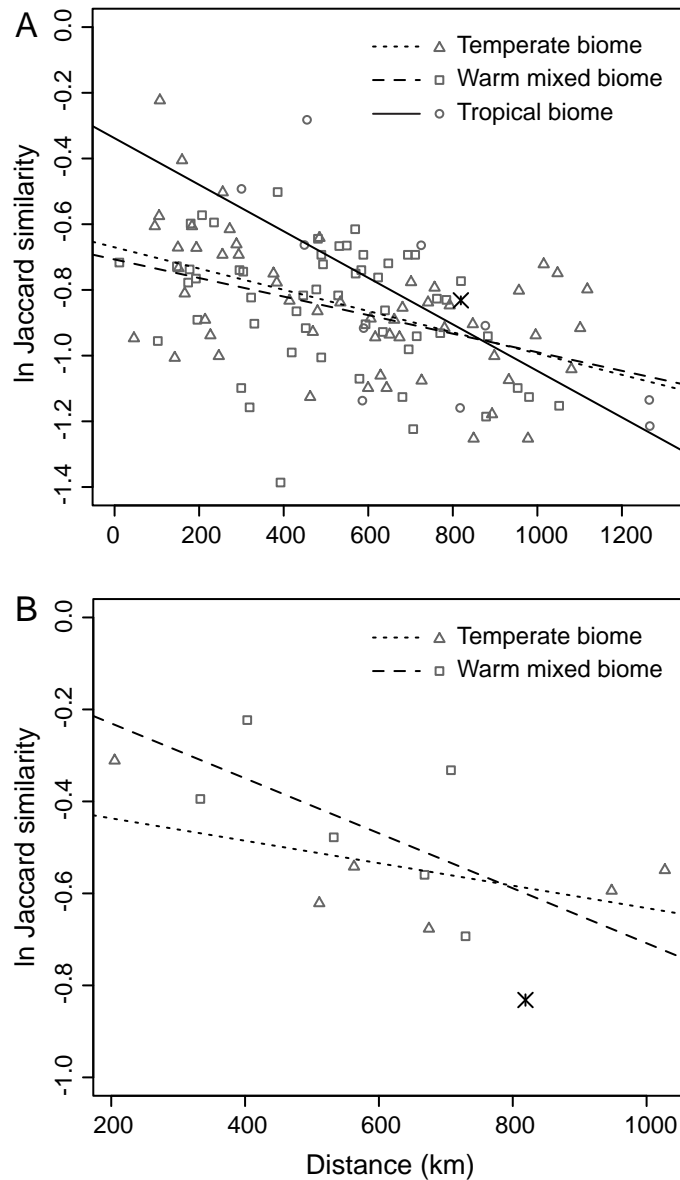


Figure 6.10. Distance-decay plots for Holocene biomes. The x-axis shows the geographical distance between samples, and the y-axis shows the natural logarithm of the Jaccard similarity coefficient. Symbols denote data points, and lines denote least-squares linear regression models. Solid line and circles, tropical forest; dashed line and squares, warm mixed forest; dotted line and triangles, temperate forest; cross, mean inter-sample compositional similarity between the Calvert Bluff and Tuscahoma Formations, plotted against the geographic distance between the formation sample midpoints. Vertical line shows bootstrapped 95% confidence interval. A, Individual Holocene sites. B, Pooled Holocene sites to simulate spatial averaging.

Table 6.3. Results for distance-decay regression of Holocene lake sites. See text for details.

	Slope	Intercept	R ² value	<i>p</i> value
Individual sites				
Temperate forests	-3.24×10 ⁻⁴	-0.67	0.26	<1×10 ⁻⁴
Warm mixed forests	-2.82×10 ⁻⁴	-0.71	0.13	0.008
Tropical forests	-7.08×10 ⁻⁴	-0.34	0.54	0.016
Combined sites				
Temperate forests	-2.44×10 ⁻⁴	-0.39	0.34	0.23
Warm mixed forests	-5.98×10 ⁻⁴	-0.11	0.35	0.22

similarity value shown is for clastic samples only; the same value for the entire data set (with the 11 lignite samples included) is -0.88, versus -0.83 for clastic samples only. This pushes the GCP data point down toward the Holocene regression line intersection in Figure 6.10A, and further away from the Holocene data in Figure 6.10B.

6.6.3 *The Paleocene GCP versus Holocene tropical and extra-tropical biomes*

Directly relating the Paleocene GCP palynoflora to the Holocene biomes depends on how the sporomorph source area for the GCP marginal marine deposits is reconstructed. If these sediments are assumed to have a sporomorph source area approximately similar to that of the Holocene lakes then the regional-scale spatial structure of the GCP vegetation was consistent with those of modern biomes. This suggests that essentially modern spatial patterns were established in plant assemblages by at least the start of the Cenozoic. Alternatively the GCP clastics had a sporomorph source considerably larger than the Holocene lakes, which means that

the spatially averaged distance-decay analyses were a better comparison. In this case the GCP flora was more heterogeneous than that of modern extra-tropical biomes. How it would relate to modern tropical vegetation requires further study.

The comparison between modern biomes has also yielded data useful for both modern and deep-time studies. Making contrasts between modern tropical and extra-tropical biomes are currently problematic because direct comparisons are scarce in the ecological literature (although see Gilbert et al., 2010). Furthermore, spatial processes that have previously been associated with hyper-diverse tropical plant communities (such as stochastic, dispersal-driven assembly [Hubbell, 2001] and density-dependent mortality of conspecifics [e.g. the Janzen-Connell hypothesis; Comita et al., 2010]) have recently been shown to be important in structuring temperate forests as well (Nakashizuka, 2001; Gazol and Ibáñez, 2009; Shibata et al., 2010; Zhang et al., 2010). These results are therefore of interest not only for relating deep-time regional-scale spatial patterns to those of the modern day, but also because they provide a valuable comparison of spatial patterns in modern tropical and extra-tropical biomes.

According to these results, tropical biomes have higher rates of spatial turnover than extra-tropical biomes, which is consistent with expectations of a latitudinal gradient in spatial turnover (Stevens, 1989; Qian and Ricklefs, 2007) that extends to the equator. The distance-decay relationship between biomes is also scale dependent, with tropical biomes being more similar at smaller spatial scales than extra-tropical biomes, despite the more rapid decline in similarity with geographic distance. These findings deserve testing more thoroughly with species-level data in

modern floras, but they potentially provide diagnostic signatures of tropical versus extra-tropical vegetation that can be recognized and assessed in the terrestrial plant fossil record.

6.7 Summary and conclusions

These results have demonstrated the importance of spatial heterogeneity in the Paleocene GCP palynoflora. A pervasive compositional separation between the Calvert Bluff and Tuscahoma Formations was revealed by all analyses, despite the presence of many geographically widespread taxa. This separation was also maintained by the lignite samples, which means that the pattern was not caused by extra-regional taxa being transported into the GCP, and is a genuine property of the regional vegetation type. A lithological separation between clastic and lignite samples, driven by both shared presences and absences of taxa among the lignites, shows the importance of taking lithological and taphonomic considerations into account when analyzing compositional variability in fossil assemblages.

The Holocene sporomorph record provides a bridge between neoecological studies of modern plant communities and shallow and deep-time paleoecological studies of those in the past (Harrington, 2004; Jaramillo et al., 2006). The combination of rate and scale dependency of spatial turnover in the Holocene biomes confounded the present efforts to associate the Paleocene GCP paratropical flora more closely with any specific modern vegetation type. Artificially increasing the spatial grain of Holocene sampling by combining samples from multiple lake cores decreased the rate of distance decay of compositional similarity, and suggests that the Paleocene

GCP flora was more heterogeneous than modern extra-tropical biomes. These results therefore illustrate the importance of both spatial grain and scale dependency in determining spatial patterns in biotic assemblages, and the potential of incorporating spatially explicit data into paleoecological studies. The Holocene data support a latitudinal gradient in spatial turnover in modern biomes, with higher levels of turnover in tropical versus extra-tropical vegetation types.

More generally, these results show that with careful analysis useful spatial data can be extracted from the fossil sporomorph record, despite low levels of taxonomic resolution imposed by pollen and spore morphology and, in the present case, the relatively low level of spatial resolution for most samples. Sporomorph data are capable of determining large-scale floral discontinuities, and taphonomic and environmental differences between samples related to lithology. Given the interest in spatial patterns and processes in modern plant communities (e.g. Hubbell, 2001; Condit et al., 2002; Duque et al., 2009; Gazol and Ibáñez, 2009), the fossil sporomorph record will be invaluable for assessing their maintenance and origins in deep time.

CHAPTER 7: AN EARLY PALAEOGENE RECORD OF EXTRA-TROPICAL PLANT DIVERSITY PATTERNS

7.1 Introduction

The tropics are the most biologically diverse regions on Earth today (Connell, 1978; Chave, 2008). A decline in species richness away from the tropics towards the poles has been recorded in all major plant and animal groups (Hillebrand, 2004); termed the latitudinal diversity gradient (LDG), this pattern is one of the most pervasive and thoroughly described large-scale biogeographic patterns (Rosenzweig, 1995; Mittelbach et al., 2007). Mechanisms for producing and maintaining tropical hyperdiversity play a key role in many models seeking to explain the LDG, which in turn is fundamental to an understanding of the spatial distribution of biodiversity across the Earth (Rosenzweig, 1995; Fine and Ree, 2006; Chave, 2008; Krug et al., 2009).

The LDG is now regarded as partly or wholly the result of latitudinal gradients in speciation, extinction and/or dispersal (Wiens and Donoghue, 2004; Goldberg et al., 2005; Jablonski et al., 2006; Mittelbach et al., 2007; Roy and Goldberg, 2007) that have been in operation over tens of millions of years, and possibly throughout much of the Phanerozoic (Ricklefs, 1987; Crane and Lidgard, 1989; Crame, 2001; Harrington, 2004; Leighton, 2005; Krug et al., 2009; Valentine and Jablonski, 2010). The tropics have an established role as a 'museum' of biodiversity (*sensu* Stebbins, 1974), in which low extinction tropical rates mean that biodiversity is accumulated and stored (Stebbins, 1974; Stephens and Wiens, 2003; Wiens and

Donoghue, 2004; Fine and Ree, 2006; Fine et al., 2008; Archibald et al., 2010). Recent research, however, has emphasised the importance of the tropics as a 'cradle' of biodiversity (*sensu* Stebbins, 1974), where high speciation and outward dispersal rates actively drive the LDG (Crane and Lidgard, 1989; Jablonski, 1993; Dynesius and Jansson, 2000; Moritz et al., 2000; Crame, 2001; Allen et al., 2002; Goldberg et al., 2005; Allen et al., 2006; Jablonski et al., 2006; Krug et al., 2009). Understanding the controls on past episodes of tropical diversification in a latitudinal context is therefore a priority for macroecologists and palaeobiologists attempting to model and explain the LDG.

One suggested cause of higher tropical diversification rates that has gained empirical support in modern biotas is that of a direct control of temperature on molecular evolution. A positive correlation between mean annual temperature (MAT) and rates of molecular evolution has been recorded for plants (Wright et al., 2003; Davies et al., 2004; Wright et al., 2006), mammals (Gillman et al., 2009) and foraminifera (Allen et al., 2006), and has been demonstrated with computer simulations (Gillooly et al., 2005). It is hypothesised that higher rates of molecular evolution in the warmer low latitudes results in higher tropical speciation rates there, which in turn drives the LDG (Allen et al., 2002; Allen et al., 2006; Allen et al., 2007). This hypothesis has far reaching implications for understanding the maintenance of the LDG over evolutionary time, and especially how the area of tropical diversification waxes and wanes in relation to changes global temperature gradients (Greenwood and Wing, 1995; Veizer et al., 2000; Fricke and Wing, 2004; Sluijs et al., 2006). However, it is not currently clear how increased mutation rates

on a microevolutionary scale manifest themselves as higher diversification rates on a macroevolutionary scale (Evans and Gaston, 2005; Mittelbach et al., 2007), and the relationship between temperature change and speciation rate along spatial and temporal gradients requires empirical testing.

The fossil record provides many 'natural experiments' in which to test the relationship between environmental and biotic change. The warming trend that occurred through the Late Paleocene and Early Eocene is an ideal case study for evaluating the impact of increased temperatures on diversification, especially in extra-tropical areas that become megathermal during greenhouse climatic phases. The GCP is well placed as a study site, because by the peak warmth of the Early Eocene it experienced a climatic regime (in terms of MAT, seasonality and precipitation) that is representative of modern tropical areas (Wolfe, 1978; Wolfe and Dilcher, 2000; Kobashi et al., 2001; Ivany et al., 2004) (see Chapter 1 section 1.3 for specific temperature estimates). Importantly, North and South America were geographically separate during this period, and the GCP was floristically distinct from the equatorial neotropics (Jaramillo and Dilcher, 2001; Harrington and Jaramillo, 2007). We can therefore examine the impacts of climate change on paratropical floral diversification largely independently of speciations and range expansions in the equatorial tropics.

Here, I test the hypothesis that increased regional temperatures directly stimulate increased speciation. Sporomorph data from the early Palaeogene of Colombia (Jaramillo and Dilcher, 2000; Jaramillo, 2002; Jaramillo et al., 2006) record an explosive diversification event, with first appearances and species richness closely

tracking global mean annual temperature (MAT) (Jaramillo et al., 2006). Most of these Early Eocene first appearances have been interpreted as *in situ* speciations (Jaramillo, 2002), and immigration into the neotropics appears to have been minimal (Jaramillo and Dilcher, 2001; Jaramillo, 2002). It is not clear whether increased temperatures directly caused this diversification, or whether the expanded area of the tropical biome at this time stimulated speciation through increased species ranges and allopatric or peripatric speciation (Rosenzweig, 1995; Jaramillo et al., 2006). If MAT did have a direct influence on the speciation rate, then speciation and species richness should increase on the GCP throughout the early Palaeogene warming trend, in concert with trends in the neotropics. The fact that seasonality and precipitation were also essentially tropical on the GCP by the Late Paleocene/Early Eocene suggests that these should not be limiting factor on diversification

Robust phylogenies and regional temperature estimates are not currently available for the GCP and the neotropics, limiting direct tests of speciation rate versus temperature in each region. However, comparing species richness and turnover in the 'permanent' tropics versus the 'temporary' paratropics in relation to changing regional and global MAT gives an indirect measure of the influence of temperature on diversification. I use a global database of sporomorph occurrences to determine whether GCP first appearances represent speciation (=global first appearances) or immigration events. I use sporomorph samples from the Colombian dataset of Jaramillo et al. (2006) as a neotropical comparison for my GCP data.

I show that (a) species richness increases on the GCP during the Late Paleocene to Early Eocene warming are suppressed compared to those in Colombia

at both within-sample and within-Age levels; (b) first and last appearance levels on the GCP do not increase through the study interval, and do not depart significantly from background levels; and (c) the proportion of GCP first appearances that are *in situ* speciation events does not increase with temperature. These results show that increasing regional MAT did not directly increase the speciation rate within the early Palaeogene GCP. This in turn does not support a primary role for increases in the rate of molecular evolution with temperature for maintaining the LDG over macroevolutionary timescales.

7.2 Materials and methods

7.2.1 Dataset description and overview

The GCP dataset extends from the Porters Creek Formation to the Zilpha Formation on the eastern US Gulf Coast (see Chapters 2 and 3 and figures therein), and thus covers ~ 17 Myr from the Middle Paleocene to the Middle Eocene. The Colombian samples of Jaramillo et al. (2006) are from the Catatumbo and Eastern Cordillera-Llanos foothills basins. They are derived from a continuous and well-dated sedimentary sequence that extends over 66 Myr from the Campanian to the Middle Miocene. The Colombian data predominantly represent coastal plain, estuarine or marginal marine sedimentation (Jaramillo, 2002; Jaramillo et al., 2006), and are therefore an appropriate taphonomic comparison for the marginal marine GCP samples (Chapter 2 and 3). The GCP dataset comprises 123 samples, 33259 specimens and 189 morphospecies. The Colombian dataset comprises 277 samples, 49972 specimens and 969 morphospecies.

Jaramillo et al. (2006) attached precise ages to each sample in their dataset, which makes it easy to extract the samples that are contemporaneous with my study interval. The GCP sedimentary sequence is less comprehensively dated, largely because there are a number of unconformities of uncertain temporal extent, which prohibit the interpolation of age estimates between dated points. Diversity comparisons between the GCP and Colombia were therefore carried out at Age level (Middle Paleocene, Late Paleocene, Early Eocene and Middle Eocene, using the Gradstein et al. [2004] timescale), to which the GCP sedimentary sequence is adequately dated (Fig. 2.1). The Zilpha Formation is uncertainly dated but the top of the sampled GCP sequence is probably ~44 Ma, which is half way through the Middle Eocene. Colombian samples were therefore only taken from the lower half of the Middle Eocene. Turnover (first and last appearance) analysis is highly vulnerable to edge effects (Foote, 2000), making a comparison between four time bins problematic (working in from the top and bottom of the section, virtually everything is an 'edge'). I have therefore only calculated first and last appearances for the GCP, where binning by formation means that eight bins are available, if the Tallahatta Formation is divided into the lower Meridian Sand Member and the upper Basic City Member to split an otherwise anomalously long time bin (see Fig. 2.1 for GCP stratigraphy).

7.2.2 Data analysis

Individual- and sample-based rarefaction

For rationale and approach see Chapter 5, section 5.3.1. Within each time

bin the species richness of the two regions was compared at two sampling levels: within-sample and within-Age (e.g. Middle Paleocene, Late Paleocene, Early Eocene and Middle Eocene), the latter of which was computed by pooling samples within each time bin. Given the low specimen counts for some samples, (Table 7.1), 50 was selected as a rarefaction level that would include most samples but would also detect differences between regions and time bins (see Fig. 3.3). Rarefying to 150 and 300 grains per sample gave qualitatively similar results, but greatly reduced the number of samples being compared, especially at the top and bottom of the section where counts are typically lower (Table 7.1). Within-Age richness was investigated using sample based rarefaction curves, to easily compare richness at different sampling intensities, among-sample heterogeneity, and sampling completeness. The data from Colombia are assembled from localities positioned more or less along a 1200 km long north-south transect (Jaramillo et al., 2006), whereas the GCP sampling localities are all within ~200 km of one another (Fig. 3.1). Larger areas are expected to harbour more taxa than small areas (Rosenzweig, 1995) (see Chapter 6, section 6.2). Therefore when using sample based rarefaction to study within-Age richness the samples were binned by locality (i.e. core or outcrop), rather than within the GCP or Colombia as a whole, to remove the influence of a species-area effect spuriously increasing species richness in the neotropics.

Within-sample evenness

This was calculated using Simpson's evenness metric (Smith and Wilson, 1996; Magurran, 2004). See Chapter 5, section 5.3.2, for rationale and calculation.

Table 7.1. Locality details and summary statistics for all GCP samples. Samples are arranged in numerical order from stratigraphically older to younger within each core/formation combination. See also sheet 'Sample_info' in Appendix 3 on the accompanying CD for core depths for each sample. N = count size, S = raw within-sample richness, R_{50} = rarefied richness at 50 grains per sample counted, R_{50} s.e. = standard error for R_{50} richness, R_{300} = rarefied richness at 300 grains per sample counted, R_{300} s.e. = standard error for R_{300} richness, Chao1 = Chao1 estimated within-sample richness, Chao1 s.e. = standard error for Chao1 estimate, $E_{1/D}$ = Simpson's measure of evenness, where $E = (1/D)/S$, and D = Simpson diversity (dominance). See text for explanation of diversity metrics shown. Only samples reaching the required count size (50 or 300 grains) have an expected rarefied richness.

Sample name	Formation	Core/locality name	N	S	R_{50}	R_{50} s.e.	R_{300}	R_{300} s.e.	Chao1	Chao1 s.e.	$E_{1/D}$
HAC/08/001	Zilpha	Harrell	145	36	22.78	2.10	-	-	43.33	6.79	0.45
HAC/08/007	Zilpha	Harrell	61	28	24.80	1.35	-	-	55.20	25.87	0.40
HAC/08/010	Zilpha	Harrell	53	29	28.02	0.79	-	-	46.00	13.48	0.60
HAC/08/013	Zilpha	Harrell	40	20	-	-	-	-	23.11	3.74	0.73
GH08/HC/045	Tallahatta - Basic City	Harrell	168	44	23.29	2.35	-	-	63.00	13.26	0.32
GH08/HC/046	Tallahatta - Basic City	Harrell	126	34	22.45	2.04	-	-	45.14	10.40	0.47
HAC/08/024	Tallahatta - Basic City	Harrell	159	35	20.64	2.08	-	-	59.00	23.32	0.44
GH08/HC/047	Tallahatta - Basic City	Harrell	113	29	20.86	1.82	-	-	47.33	28.64	0.47
GH00/Ha/090	Tallahatta - Basic City	Harrell	53	24	23.20	0.75	-	-	54.33	43.99	0.65
GH00/Ha/089	Tallahatta - Basic City	Harrell	79	28	23.82	1.50	-	-	31.11	3.74	0.72
GH00/Ha/088	Tallahatta - Basic City	Harrell	308	47	20.60	2.38	46.61	0.61	58.67	9.57	0.21
GH00/Ha/087	Tallahatta - Basic City	Harrell	200	41	23.36	2.22	-	-	50.43	9.17	0.33
GH00/Ha/085	Tallahatta - Meridian	Harrell	323	33	13.63	2.09	32.12	0.89	42.43	9.17	0.14
GH00/Ha/083	Tallahatta - Meridian	Harrell	95	28	20.17	1.86	-	-	39.14	10.40	0.29
GH00/Ht/078A	Hatchetigbee	Harrell	326	39	17.00	2.16	37.83	1.01	49.11	8.60	0.18
GH00/Ht/074	Hatchetigbee	Harrell	362	46	16.25	2.31	42.27	1.71	63.27	11.83	0.12
GH00/Ht/071A	Hatchetigbee	Harrell	327	38	17.25	2.19	37.05	0.92	45.86	8.00	0.18
GH00/Ht/057A	Hatchetigbee	Harrell	336	40	16.27	2.24	38.40	1.17	49.10	7.61	0.17
GH00/Ht/047	Hatchetigbee	Harrell	357	39	15.60	2.19	36.66	1.38	46.09	6.13	0.17

Sample name	Formation	Core/locality name	N	S	R ₅₀	R ₅₀ s.e.	R ₃₀₀	R ₃₀₀ s.e.	Chao1	Chao1 s.e.	E _{1/D}
GH00/Ht/036	Hatchetigbee	Harrell	357	45	16.84	2.31	41.78	1.60	66.38	16.15	0.18
GH00/Ht/026	Hatchetigbee	Harrell	420	35	13.74	2.00	30.76	1.73	48.00	12.72	0.14
GH00/Ht/013A	Hatchetigbee	Harrell	346	21	9.39	1.65	20.00	0.93	25.20	6.08	0.23
GH00/Ht/001A	Hatchetigbee	Harrell	314	33	13.82	2.00	32.36	0.76	44.38	9.90	0.18
WAH/08/079	Hatchetigbee	OSM#2 Wahalak	336	43	18.51	2.28	41.40	1.17	52.10	7.61	0.22
WAH/08/077	Hatchetigbee	OSM#2 Wahalak	318	40	16.14	2.26	39.13	0.89	53.13	11.04	0.19
WAH/08/075	Hatchetigbee	OSM#2 Wahalak	321	43	16.37	2.30	41.84	1.01	54.33	8.33	0.14
WAH/08/074	Hatchetigbee	OSM#2 Wahalak	282	38	15.01	2.22	-	-	72.20	31.35	0.17
WAH/08/073	Hatchetigbee	OSM#2 Wahalak	219	34	15.12	2.15	-	-	51.00	13.48	0.16
WAH/08/072	Hatchetigbee	OSM#2 Wahalak	323	42	15.87	2.29	40.81	1.02	52.91	8.38	0.18
WAH/08/071	Hatchetigbee	OSM#2 Wahalak	314	38	15.24	2.25	37.44	0.72	43.08	4.58	0.18
WAH/08/070	Hatchetigbee	OSM#2 Wahalak	283	44	19.24	2.39	-	-	52.27	6.84	0.20
WAH/08/069	Hatchetigbee	OSM#2 Wahalak	308	41	17.50	2.27	40.66	0.57	47.50	5.59	0.22
WAH/08/068	Hatchetigbee	OSM#2 Wahalak	309	45	17.71	2.34	44.47	0.70	57.75	9.09	0.20
WAH/08/067	Hatchetigbee	OSM#2 Wahalak	307	44	17.85	2.37	43.61	0.60	66.67	19.81	0.17
WAH/08/066	Hatchetigbee	OSM#2 Wahalak	331	42	17.72	2.26	40.37	1.18	69.20	25.87	0.20
WAH/08/065	Hatchetigbee	OSM#2 Wahalak	214	38	18.04	2.31	-	-	55.50	16.09	0.21
WAH/08/064	Hatchetigbee	OSM#2 Wahalak	190	40	20.04	2.32	-	-	57.00	13.48	0.27
WAH/08/063	Hatchetigbee	OSM#2 Wahalak	249	39	18.55	2.25	-	-	50.38	9.90	0.25
WAH/08/062	Hatchetigbee	OSM#2 Wahalak	325	38	17.59	2.24	37.27	0.81	42.50	5.04	0.15
WAH/08/061	Tuscahoma	OSM#2 Wahalak	623	21	8.24	1.65	17.44	1.46	22.50	3.49	0.08
WAH/08/060	Tuscahoma	OSM#2 Wahalak	319	35	15.74	2.12	34.33	0.78	44.17	9.73	0.25
WAH/08/059	Tuscahoma	OSM#2 Wahalak	458	44	14.34	2.19	36.12	2.25	67.75	17.56	0.07
WAH/08/057	Tuscahoma	OSM#2 Wahalak	795	38	10.48	1.98	25.55	2.36	49.38	9.90	0.05
WAH/08/054	Tuscahoma	OSM#2 Wahalak	301	40	18.90	2.26	39.96	0.19	46.88	6.82	0.22
WAH/08/052	Tuscahoma	OSM#2 Wahalak	313	32	15.10	2.00	31.58	0.63	39.50	8.37	0.28
GH08/Wa/051	Tuscahoma	OSM#2 Wahalak	396	45	15.11	2.27	39.76	1.96	60.55	10.92	0.09
GH08/Wa/048	Tuscahoma	OSM#2 Wahalak	316	38	14.78	2.25	37.27	0.81	48.11	8.60	0.16

Sample name	Formation	Core/locality name	N	S	R ₅₀	R ₅₀ s.e.	R ₃₀₀	R ₃₀₀ s.e.	Chao1	Chao1 s.e.	E _{1/D}
GH08/Wa/046	Tuscahoma	OSM#2 Wahalak	309	45	17.15	2.39	44.50	0.68	56.33	8.33	0.11
GH08/Wa/043	Tuscahoma	OSM#2 Wahalak	281	28	12.06	1.97	-	-	33.00	5.17	0.18
GH08/Wa/041	Tuscahoma	OSM#2 Wahalak	334	40	14.22	2.25	38.09	1.27	59.13	14.79	0.14
GH08/Wa/038	Tuscahoma	OSM#2 Wahalak	233	31	14.71	2.12	-	-	35.50	4.62	0.20
GH08/Wa/036	Tuscahoma	OSM#2 Wahalak	322	35	13.50	2.12	33.95	0.97	50.00	13.08	0.17
GH08/Wa/034	Tuscahoma	OSM#2 Wahalak	308	49	15.96	2.40	48.27	0.81	83.36	20.31	0.14
WAH/08/047	Tuscahoma	OSM#2 Wahalak	287	55	22.62	2.53	-	-	67.21	8.32	0.20
WAH/08/044	Tuscahoma	OSM#2 Wahalak	311	36	16.37	2.19	35.64	0.58	41.63	5.90	0.17
WAH/08/043	Tuscahoma	OSM#2 Wahalak	472	42	14.95	2.26	36.07	1.97	51.75	8.82	0.07
WAH/08/038	Tuscahoma	OSM#2 Wahalak	314	49	18.67	2.42	48.09	0.90	63.62	9.77	0.19
WAH/08/037	Tuscahoma	OSM#2 Wahalak	389	40	13.82	2.26	36.13	1.70	53.13	11.04	0.11
WAH/08/036	Tuscahoma	OSM#2 Wahalak	307	46	19.31	2.32	45.56	0.63	67.38	16.15	0.22
WAH/08/032	Tuscahoma	OSM#2 Wahalak	309	44	18.71	2.31	43.50	0.68	61.00	13.48	0.22
WAH/08/026	Tuscahoma	OSM#2 Wahalak	233	35	16.60	2.16	-	-	45.11	8.60	0.20
WAH/08/023	Tuscahoma	OSM#2 Wahalak	307	43	18.70	2.31	42.66	0.57	58.00	13.08	0.22
GH08/Wa/028	Tuscahoma	OSM#2 Wahalak	347	44	15.79	2.30	41.17	1.52	71.14	20.99	0.12
GH08/Wa/027	Tuscahoma	OSM#2 Wahalak	331	32	14.08	2.05	31.01	0.93	38.43	6.91	0.19
GH08/Wa/024	Tuscahoma	OSM#2 Wahalak	269	44	16.47	2.37	-	-	75.63	22.14	0.12
GH00/AC/013	Tuscahoma	Red Hills Mine	359	39	17.94	2.12	36.73	1.35	54.60	16.43	0.19
GH00/AC/012	Tuscahoma	Red Hills Mine	302	35	15.98	2.04	34.90	0.31	56.00	20.90	0.22
GH00/AC/011A	Tuscahoma	Red Hills Mine	326	43	18.20	2.32	41.83	1.02	52.10	7.61	0.22
GH00/AC/009	Tuscahoma	Red Hills Mine	1368	30	7.27	1.74	18.21	2.11	37.00	10.27	0.05
GH00/AC/008	Tuscahoma	Red Hills Mine	390	47	17.04	2.41	42.78	1.78	59.00	9.34	0.17
GH00/AC/006	Nanafalia	Red Hills Mine	400	31	13.93	1.92	28.21	1.44	40.00	10.68	0.21
GH00/AC/004	Nanafalia	Red Hills Mine	896	35	9.31	1.95	22.92	2.16	70.00	49.82	0.05
GH00/AC/002	Nanafalia	Red Hills Mine	330	29	12.77	1.95	27.98	0.95	47.33	28.64	0.18
GH08/KC/001	Nanafalia	Knight	314	43	18.09	2.33	42.40	0.74	50.80	6.80	0.19
GH08/KC/006	Nanafalia	Knight	194	42	21.32	2.33	-	-	57.00	12.23	0.14

Sample name	Formation	Core/locality name	N	S	R ₅₀	R ₅₀ s.e.	R ₃₀₀	R ₃₀₀ s.e.	Chao1	Chao1 s.e.	E _{1/D}
GH08/KC/015	Nanafalia	Knight	47	14	-	-	-	-	19.60	7.48	0.31
GH08/KC/017	Nanafalia	Knight	188	42	20.22	2.33	-	-	75.00	24.64	0.22
GH08/KC/020	Nanafalia	Knight	162	31	18.78	1.99	-	-	47.50	20.20	0.26
GH08/KC/021	Nanafalia	Knight	149	29	15.75	2.07	-	-	46.50	16.09	0.17
GH08/KC/022	Nanafalia	Knight	265	29	11.71	2.03	-	-	51.75	26.33	0.11
GH08/KC/026	Nanafalia	Knight	215	42	18.35	2.36	-	-	68.25	19.03	0.11
GH08/Wa/018	Nanafalia	OSM#2 Wahalak	115	33	20.91	2.08	-	-	63.60	28.55	0.34
GH08/Wa/017	Nanafalia	OSM#2 Wahalak	166	31	16.43	2.12	-	-	44.00	11.71	0.13
GH08/Wa/016	Nanafalia	OSM#2 Wahalak	226	35	15.78	2.16	-	-	57.67	19.81	0.14
GH08/Wa/015	Nanafalia	OSM#2 Wahalak	108	24	16.05	1.84	-	-	33.17	9.73	0.25
GH08/Wa/013	Nanafalia	OSM#2 Wahalak	404	46	17.43	2.33	41.32	1.84	61.00	12.23	0.10
GH08/Wa/012	Nanafalia	OSM#2 Wahalak	334	49	18.53	2.36	46.59	1.42	80.63	22.14	0.11
GH08/Wa/011	Nanafalia	OSM#2 Wahalak	329	48	16.91	2.34	45.81	1.36	73.09	15.81	0.12
GH08/Wa/010	Nanafalia	OSM#2 Wahalak	210	30	16.05	2.06	-	-	35.14	5.88	0.16
GH08/Wa/009	Nanafalia	OSM#2 Wahalak	264	38	17.42	2.19	-	-	47.10	7.61	0.22
GH08/Wa/007	Nanafalia	OSM#2 Wahalak	95	26	18.47	1.83	-	-	48.75	26.33	0.32
GH08/Wa/006	Nanafalia	OSM#2 Wahalak	249	43	21.50	2.25	-	-	63.00	17.90	0.28
GH08/Wa/005	Nanafalia	OSM#2 Wahalak	293	45	19.47	2.33	-	-	57.00	9.34	0.21
GH08/Wa/004	Naheola	OSM#2 Wahalak	330	37	14.83	2.24	35.92	0.97	42.50	5.31	0.15
WAH/08/019	Naheola	OSM#2 Wahalak	119	29	17.38	2.06	-	-	46.14	14.52	0.25
WAH/08/016	Naheola	OSM#2 Wahalak	82	24	16.90	1.84	-	-	58.00	36.98	0.24
WAH/08/011	Naheola	OSM#2 Wahalak	115	31	19.78	2.05	-	-	44.13	11.04	0.27
WAH/08/003	Naheola	OSM#2 Wahalak	328	41	17.34	2.31	39.92	0.98	48.33	6.79	0.19
WAH/08/001	Naheola	OSM#2 Wahalak	138	24	13.41	1.88	-	-	59.00	49.82	0.21
JDC/08/066	Naheola	Jasper Deep Core	84	24	17.22	1.80	-	-	45.00	20.90	0.26
JDC/08/054	Naheola	Jasper Deep Core	99	26	18.36	1.84	-	-	35.43	9.17	0.36
JDC/08/050	Naheola	Jasper Deep Core	124	29	17.77	2.01	-	-	50.00	20.90	0.17
JDC/08/043	Naheola	Jasper Deep Core	317	48	21.37	2.32	47.02	0.94	69.86	17.62	0.27

Sample name	Formation	Core/locality name	N	S	R ₅₀	R ₅₀ s.e.	R ₃₀₀	R ₃₀₀ s.e.	Chao1	Chao1 s.e.	E _{1/D}
JDC/08/037	Naheola	Jasper Deep Core	148	36	20.39	2.17	-	-	66.60	28.55	0.19
JDC/08/024	Naheola	Jasper Deep Core	214	40	18.33	2.28	-	-	67.14	20.99	0.17
JDC/08/011	Naheola	Jasper Deep Core	81	23	18.54	1.55	-	-	28.14	5.88	0.40
JDC/08/001	Naheola	Jasper Deep Core	67	21	18.03	1.35	-	-	26.63	5.90	0.33
TUC/08/026	Naheola	OSM#1 Tuckabum	156	21	13.17	1.75	-	-	23.50	3.85	0.26
TUC/08/024	Naheola	OSM#1 Tuckabum	323	31	14.46	2.05	30.47	0.70	33.63	3.50	0.20
TUC/08/023	Naheola	OSM#1 Tuckabum	319	35	14.36	2.08	34.09	0.91	50.00	13.08	0.17
TUC/08/022	Naheola	OSM#1 Tuckabum	152	24	13.72	1.85	-	-	40.50	20.20	0.27
TUC/08/021	Naheola	OSM#1 Tuckabum	347	41	14.89	2.32	39.01	1.29	47.00	5.14	0.12
TUC/08/020	Naheola	OSM#1 Tuckabum	417	40	11.97	2.19	34.13	2.02	68.50	23.90	0.09
TUC/08/016	Porters Creek	OSM#1 Tuckabum	248	33	13.91	2.12	-	-	50.14	14.52	0.17
TUC/08/013	Porters Creek	OSM#1 Tuckabum	310	38	13.77	2.21	37.38	0.75	66.50	23.90	0.14
TUC/08/031	Porters Creek	OSM#1 Tuckabum	128	20	12.26	1.71	-	-	47.50	71.08	0.22
TUC/08/012	Porters Creek	OSM#1 Tuckabum	175	25	13.45	1.94	-	-	31.43	6.91	0.21
TUC/08/010	Porters Creek	OSM#1 Tuckabum	237	26	11.47	1.87	-	-	37.14	10.40	0.13
TUC/08/009	Porters Creek	OSM#1 Tuckabum	142	23	12.79	1.88	-	-	62.00	97.07	0.16
TUC/08/008	Porters Creek	OSM#1 Tuckabum	139	24	13.22	1.92	-	-	42.20	18.60	0.20
TUC/08/007	Porters Creek	OSM#1 Tuckabum	107	16	11.09	1.52	-	-	21.25	8.28	0.21
TUC/08/004	Porters Creek	OSM#1 Tuckabum	119	30	18.40	2.05	-	-	64.00	36.98	0.27
TUC/08/003	Porters Creek	OSM#1 Tuckabum	131	28	16.39	2.02	-	-	49.00	20.90	0.23

Species richness estimation

Observed species richness is influenced directly by sample size. While rarefaction procedures allow samples of different sizes to be compared fairly for species richness, these may be biased by differences in relative abundance distributions between samples, or by differences in among-sample heterogeneity between groups of samples (Tipper, 1979; Lande et al., 2000; Magurran, 2004). Rarefaction methods also do not give an accurate depiction of true species richness when sampling is incomplete (Gotelli and Colwell, 2001; Magurran, 2004), which is likely to be the case in highly diverse assemblages such as the GCP and Colombian pollen records that have many rare taxa (Harrington, 2001; Jaramillo, 2002; Harrington et al., 2004; Harrington and Jaramillo, 2007; see also chapters 4, 5 and Appendix 1). Species richness estimators provide an alternative means of comparing richness among samples or groups of samples, and also supply information on the total number of species within a sampling unit.

Although a variety of richness estimation techniques have been developed (reviewed in Colwell and Coddington, 1994; Magurran, 2004) the most effective are nonparametric methods, which are appropriate for fossil data as discussed by Harrington and Jaramillo (2007). These do not assume any underlying species abundance models (hence nonparametric), are efficient to compute, and provide an estimate of variance for computing confidence intervals (Magurran, 2004). As with the rarefied data, species richness was estimated at the within-sample and within-Age levels. Several nonparametric species richness estimators for both abundance and occurrence data are computed in the R package Vegan (Oksanen et al., 2010),

all of which gave qualitatively similar results with the current data. Here, I present results for the Chao1 estimator for abundance data (applied to within-sample richness estimation), and the Chao2 estimator for occurrence data (applied to within-Age richness estimation using pooled samples). The Chao1 estimator is computed as $S_{\text{Chao1}} = S_{\text{obs}} + (F_1^2/2F_2)$, where S_{obs} = the number of species in the sample, F_1 = the number of observed species represented by a single individual (singletons), and F_2 = the number of observed species represented by two individuals (Magurran, 2004). The Chao2 estimator is computed as $S_{\text{Chao2}} = S_{\text{obs}} + (Q_1^2/2Q_2)$, where Q_1 = the number of observed species that occur in one sample only (uniques), and Q_2 = the number of observed species that occur in two samples (Colwell and Coddington, 1994; Magurran, 2004). Sampling is considered to be complete when all taxa are either represented by at least two individuals (for abundance data) or are present in at least two samples (for incidence data) (Colwell and Coddington, 1994; Magurran, 2004).

Non-metric multidimensional scaling (NMDS)

For rationale and approach see Chapter 5, section 5.3.3. The samples were ordinated using log transformed, Wisconsin standardised data with the Bray-Curtis dissimilarity metric (see Chapter 5, page 109). I have ordinated the data to study major compositional trends among samples, to determine any major stratigraphic breaks that may indicate periods of major compositional change, and to provide a complement to turnover analysis.

Proportional first and last appearances

Given the uneven levels of sampling intensity through the section (Table 7.1, Fig. 3.3) I have subsampled the data prior to tabulating turnover levels. The procedure is analogous to the rarefaction techniques used to study species richness (detailed above), but differs in using randomized resampling rather than the analytical subsampling solutions available for conventional rarefaction (Hurlbert, 1971; Heck et al., 1975; Colwell et al., 2004). This is necessary to preserve taxon identities for computing first and last appearances.

The samples were pooled together within formations, and then 290 individuals were drawn from each formation. This number is low given the sample size of some formations within the dataset (Fig. 3.3), but represents the highest subsampling level that can be used for all formations to be included. All taxa that were limited to one formation were excluded, and then the numbers of first and last appearances in each formation were calculated, with the assumption that a taxon ranges through to its final occurrence, even if it is not present in all the intervening formations. The numbers of first and last appearances in each formation were then divided by the standing richness, that is, the number of range through taxa that are present in each formation. Turnover was expressed in this way (i.e. proportionally) to ensure that the levels were not biased by varying numbers of taxa in each formation (Foote and Miller, 2007). Given the uncertainty of dating many of the formation boundaries precisely, no effort was made to further divide the proportional turnover by time-interval length to study rates of first and last appearances, or to calculate per capita rates (Foote, 2000). This whole procedure was repeated 1000 times, and the

mean proportional first and last appearance levels calculated for each formation.

Although turnover values were calculated for each formation, those from the Porters Creek and Zilpha formations (the stratigraphically highest and lowest formations in the section) were discounted from the analyses because they are entirely biased by edge effects (Foote, 2000). In the Porters Creek Formation all taxa are necessarily first appearances, giving a 100% origination value. Similarly, all taxa in the Zilpha Formation are necessarily last appearances, spuriously suggesting a 100% extinction at the top of the section. As taxa limited to one formation were excluded from the calculations, there can be no first appearances in the Zilpha Formation, and no last appearances in the Porters Creek Formation.

To test objectively if turnover levels exceeded background levels in any formation, a simple null model was constructed following the procedure described by Olszewski and Patzkowsky (2001a). The total number of first (or last) appearances for the section (aside from those in the Porters Creek and Zilpha formations) was divided by the total number of range through occurrences, which gives the probability that any occurrence is a first (or last) appearance. This was carried out separately for each of the 1000 subsampling runs, and the mean taken. This value was used as the expected proportional origination (or extinction) within each formation, assuming that levels of first and last appearances were constant throughout.

Binomial 95% confidence intervals were fitted to this proportion, using the equation $CI = 1.96 \times (p(1-p)/n)^{1/2}$, where p = the null (expected) proportional first (or last) appearance, and n = the sample size (in this case the mean standing richness from all 1000 subsampling runs, for each formation). Any observed first or last appearance

levels falling above or below the confidence intervals are significantly higher or lower, respectively, than the background turnover level.

Origins of first appearances: speciation versus immigration

I used the John Williams Index of Palaeopalynology (JWIP) to search for other occurrences of published form species, to determine whether first appearances were speciation or immigration events. The JWIP is a card catalogue that is curated and maintained by John Williams at the Natural History Museum, London. It contains occurrence data for sporomorph form species in the palynological literature, along with the country and age estimate (typically resolved to age or epoch level) for each occurrence. Known synonyms (see Appendix 1) were searched for in addition to the form species names used in this thesis. All taxa were classified into one of four main groups (taxon ranges and first appearance classifications are provided in Table 7.2):

1. Generalised taxa: morphotypes that have not been counted at form species level, such as *Deltoidospora* spp., the Betulaceae/Myricaceae type, and bisaccate pollen. Treated as uninformative for the present question.

2. Already present on the GCP: form species that are known to range down into the Early Paleocene and/or Cretaceous on the GCP. Treated as uninformative for the present question.

3. Immigrant taxa: form species that have earlier published occurrences outside of the GCP. Subdivided by geographical area – North America (NA), South America (SA), Europe (E), Africa (A), and widespread (W). This latter category is for cosmopolitan taxa that have multiple global occurrences immediately prior to their

Table 7.2. Taxon range and first appearance data for GCP taxa in this dataset. First and last appearances are given at the formation level. For immigration/speciation tabulations, G = generalised type, C = already present on the GCP prior to the study interval, GCP = speciation (recorded first appearance datum is earliest global occurrence for this taxon), N = 'New' (taxa that have not been found in the published literature, and are being treated as new species and possible speciations), N.am = immigration from elsewhere in North America, S.am = immigration from South America, E = immigration from Europe, W = immigrant taxon with widespread geographic range.

Taxon	First appearance	Last appearance	Immigration/ speciation
<i>Acer? striatellum</i>	Hatchetigbee	Hatchetigbee	W
<i>Aesculiidites circumstriatus</i>	Naheola	Zilpha	W
<i>Ailanthipites berryi</i>	Naheola	Tallahatta	W
<i>Alnus scoticus</i>	Naheola	Hatchetigbee	N.am
<i>Alnus verus</i>	Porters Creek	Zilpha	C
<i>Appendicisporites</i> spp.	Porters Creek	Porters Creek	G
<i>Aquilapollenites attenuatus</i>	Porters Creek	Hatchetigbee	C
<i>Aquilapollenites</i> sp.3	Porters Creek	Porters Creek	N
<i>Aquilapollenites</i> sp.4	Nanafalia	Nanafalia	N
<i>Aquilapollenites</i> sp.5	Nanafalia	Nanafalia	N
<i>Aquilapollenites</i> sp.6	Nanafalia	Nanafalia	N
<i>Aquilapollenites</i> sp.7	Hatchetigbee	Hatchetigbee	N
<i>Arecipites</i> spp.	Porters Creek	Tallahatta	G
<i>Baculatisporites primarus</i>	Porters Creek	Hatchetigbee	W
<i>Basopollis obscurcostatus</i>	Porters Creek	Meridian	GCP
Betulaceae/Myricaceae type	Porters Creek	Zilpha	G
Bisaccate pollen	Porters Creek	Zilpha	G
<i>Boehlensipollis minimus</i>	Hatchetigbee	Hatchetigbee	N.am
<i>Boehlensipollis verrucata</i>	Hatchetigbee	Hatchetigbee	GCP
<i>Bombacacidites nacimientoensis</i>	Porters Creek	Hatchetigbee	N.am
<i>Bombacacidites reticulatus</i>	Porters Creek	Meridian	C
<i>Bombacacidites</i> sp.1	Hatchetigbee	Hatchetigbee	N
<i>Bombacacidites</i> sp.1 of Frederiksen 1988	Naheola	Zilpha	GCP
<i>Brosipollis striata</i>	Hatchetigbee	Zilpha	E
<i>Bullasporis</i> spp.	Nanafalia	Hatchetigbee	G
c.f. <i>Symplocoipollenites</i> sp. of Elsik 1968	Porters Creek	Hatchetigbee	G
<i>Camarazonosporites heskamensis</i>	Tusahoma	Tallahatta	GCP
<i>Camarazonosporites</i> sp.1	Nanafalia	Nanafalia	N
<i>Camarazonosporites grootii</i>	Porters Creek	Hatchetigbee	GCP
<i>Caprifoliipites</i> sp.1	Zilpha	Zilpha	N
<i>Caprifoliipites</i> sp.4	Tallahatta	Tallahatta	N
<i>Caprifoliipites</i> sp.5	Naheola	Nanafalia	N

Taxon	First appearance	Last appearance	Immigration/ speciation
<i>Caprifoliipites</i> spp.	Naheola	Zilpha	G
<i>Caryapollenites imparalis</i>	Naheola	Zilpha	N.am
<i>Caryapollenites veripites</i>	Naheola	Zilpha	N.am
<i>Caryapollenites wodehousei</i>	Nanafalia	Tallahatta	N.am
<i>Celtis tschudyi</i> group	Hatchetigbee	Zilpha	N.am
<i>Chenopodipollis</i> sp.	Porters Creek	Zilpha	G
<i>Choanopollenites alabamicus</i>	Porters Creek	Nanafalia	C
<i>Choanopollenites conspicuus</i>	Porters Creek	Tusahoma	C
<i>Choanopollenites discipulus</i>	Porters Creek	Porters Creek	C
<i>Choanopollenites patricius</i>	Nanafalia	Nanafalia	GCP
<i>Cicatricosisporites dorogensis</i>	Porters Creek	Tallahatta	C
<i>Cingulatisporites</i> sp.	Porters Creek	Zilpha	G
<i>Complexiopollis</i> spp.	Porters Creek	Meridian	G
<i>Compositoipollenites</i> sp.1	Nanafalia	Nanafalia	N
<i>Compositoipollenites</i> sp.2	Meridian	Meridian	N
<i>Cupressacites hiatipites</i>	Porters Creek	Zilpha	C
<i>Cupuliferoideaepollenites</i> spp.	Tusahoma	Zilpha	G
<i>Cupuliferoipollenites</i> spp.	Naheola	Zilpha	G
<i>Cycadopites follicularis</i>	Porters Creek	Zilpha	C
<i>Deltoidospora</i> spp.	Porters Creek	Zilpha	G
<i>Dicolpopollis</i> spp.	Hatchetigbee	Hatchetigbee	G
<i>Ephedripites</i> spp.	Porters Creek	Tallahatta	G
<i>Erdtmanipollis cretaceus</i>	Porters Creek	Hatchetigbee	N.am
<i>Ericipites</i> spp.	Naheola	Zilpha	G
<i>Eucommia</i> spp.	Porters Creek	Zilpha	G
<i>Favitricolporites baculoferus</i>	Porters Creek	Zilpha	C
<i>Favitricolporites</i> sp.1	Hatchetigbee	Tallahatta	N
<i>Favitricolporites</i> sp.2	Hatchetigbee	Hatchetigbee	N
<i>Favitricolporites</i> sp.3	Tusahoma	Tusahoma	N
<i>Foveotricolpites</i> sp.1	Zilpha	Zilpha	N
<i>Fraxinoipollenites</i> sp.1	Tusahoma	Tusahoma	N
<i>Gleicheniidites senonicus</i>	Porters Creek	Hatchetigbee	W
<i>Granulatisporites luteticus</i>	Hatchetigbee	Tallahatta	E
<i>Holkopollenites chemardensis</i>	Porters Creek	Tusahoma	C
<i>Horniella brevicolpata</i>	Hatchetigbee	Zilpha	GCP
<i>Horniella</i> sp.1	Hatchetigbee	Hatchetigbee	N
<i>Horniella</i> spp.	Naheola	Tallahatta	G
<i>Ilexpollenites</i> spp.	Tallahatta	Zilpha	G
<i>Insulapollenites rugulatus</i>	Porters Creek	Hatchetigbee	N.am
<i>Interpollis microsupplingensis</i>	Hatchetigbee	Tallahatta	E
<i>Interpollis paleocenicus</i>	Naheola	Naheola	C

Taxon	First appearance	Last appearance	Immigration/ speciation
<i>Intratropopollenites instructus</i>	Hatchetigbee	Zilpha	E
<i>Intratropopollenites pseudoinstructus</i>	Porters Creek	Zilpha	C
<i>Intratropopollenites vespites</i>	Naheola	Tallahatta	N.am
<i>Juglans nigripites</i>	Tallahatta	Tallahatta	N.am
<i>Kyandopollenites anneratus</i>	Tusahoma	Tusahoma	N.am
<i>Laevigatosporites haardtii</i>	Porters Creek	Zilpha	C
<i>Lanagiopollis crassa</i>	Tallahatta	Tallahatta	S.am
<i>Lanagiopollis cribellata</i>	Naheola	Tusahoma	C
<i>Lanagiopollis eocaenica</i>	Tallahatta	Zilpha	G
<i>Lanagiopollis hadrodictya</i>	Tallahatta	Tallahatta	GCP
<i>Lanagiopollis lihoka</i>	Naheola	Hatchetigbee	N.am
<i>Lanagiopollis</i> sp.1	Tusahoma	Tusahoma	N
<i>Lanagiopollis</i> sp.2	Hatchetigbee	Hatchetigbee	N
<i>Leiotriletes</i> spp.	Porters Creek	Zilpha	G
<i>Liliacidites</i> spp.	Porters Creek	Zilpha	G
<i>Longapertites</i> spp.	Nanafalia	Zilpha	S.am
<i>Malvacipollis</i> spp.	Tusahoma	Zilpha	G
<i>Matanomadhiasulcites maximus</i>	Nanafalia	Tallahatta	S.am
<i>Microfoveolatisporites pseudodentatus</i>	Porters Creek	Tallahatta	C
<i>Microreticulatisporites</i> spp.	Porters Creek	Hatchetigbee	G
<i>Milfordia hungaricus</i>	Hatchetigbee	Tallahatta	E
<i>Milfordia minima</i>	Hatchetigbee	Tallahatta	E
<i>Momipites anellus</i>	Naheola	Hatchetigbee	N.am
<i>Momipites</i> cf. <i>M. flexus</i> of Frederiksen 1998	Naheola	Hatchetigbee	GCP
<i>Momipites coryloides</i>	Porters Creek	Zilpha	C
<i>Momipites microfoveolatus</i>	Porters Creek	Zilpha	C
<i>Momipites nicholsii</i>	Tallahatta	Tallahatta	GCP
<i>Momipites strictus</i>	Porters Creek	Tusahoma	C
<i>Momipites triradiatus</i>	Naheola	Hatchetigbee	C
<i>Momipites ventifluminis</i>	Tusahoma	Tallahatta	C
<i>Momipites waltmanensis</i>	Naheola	Hatchetigbee	C
<i>Monocolpopollenites tranquillus</i>	Porters Creek	Tallahatta	C
<i>Myriophyllum</i> sp. of Frederiksen 1980	Zilpha	Zilpha	GCP
<i>Nudopollis endangulatus</i>	Naheola	Tusahoma	W
<i>Nudopollis terminalis</i>	Porters Creek	Zilpha	C
<i>Nudopollis thiergaartii</i>	Naheola	Tallahatta	C
<i>Nuxpollenites crockettensis</i>	Hatchetigbee	Hatchetigbee	GCP
<i>Nuxpollenites psilatus</i>	Hatchetigbee	Hatchetigbee	GCP
<i>Nyssa kruschii</i>	Porters Creek	Zilpha	W
<i>Nyssapollenites paleocenicus</i>	Porters Creek	Porters Creek	N.am
<i>Nyssapollenites pulvinus</i>	Hatchetigbee	Hatchetigbee	GCP

Taxon	First appearance	Last appearance	Immigration/ speciation
<i>Nyssapollenites</i> spp.	Porters Creek	Zilpha	G
<i>Paraalnipollenites confusus</i>	Nanafalia	Hatchetigbee	C
<i>Patellasporites</i> spp.	Porters Creek	Naheola	G
<i>Pentacolporate</i> sp. 1	Hatchetigbee	Hatchetigbee	N
<i>Pistillipollenites mcgregorii</i>	Nanafalia	Zilpha	W
<i>Platanus occidentaloides</i>	Zilpha	Zilpha	GCP
<i>Platycarya platycaryoides</i>	Hatchetigbee	Zilpha	E
<i>Platycaryapollenites</i> spp.	Hatchetigbee	Zilpha	G
<i>Polyatriopollenites stellatus</i>	Porters Creek	Zilpha	C
<i>Porocolpopollenites ollivierae</i>	Nanafalia	Tallahatta	N.am
<i>Porocolpopollenites</i> sp. 1	Nanafalia	Nanafalia	N
<i>Porocolpopollenites</i> sp. 2	Tusahoma	Tusahoma	N
<i>Porocolpopollenites</i> sp. 3	Naheola	Tusahoma	N
<i>Porocolpopollenites</i> sp. 4	Nanafalia	Nanafalia	N
<i>Proxapertites psilate</i> type	Naheola	Zilpha	S.am
<i>Proxapertites reticulate</i> type	Hatchetigbee	Tallahatta	S.am
<i>Pseudoplicapollis limitata</i>	Porters Creek	Tusahoma	C
<i>Pseudoplicapollis serenus</i>	Porters Creek	Porters Creek	C
<i>Punctatisporites</i> spp.	Tusahoma	Hatchetigbee	G
<i>Quadrupollenites vagus</i>	Naheola	Hatchetigbee	GCP
<i>Reticuloidosporites</i> spp.	Porters Creek	Meridian	G
<i>Retitrescolpites anguloluminosus</i>	Naheola	Tusahoma	N.am
<i>Retitrescolpites</i> sp. 1	Nanafalia	Nanafalia	N
<i>Retitriletes</i> spp.	Porters Creek	Tallahatta	G
<i>Rhoipites bradleyi</i>	Nanafalia	Tusahoma	GCP
<i>Rhoipites capax</i>	Zilpha	Zilpha	GCP
<i>Rhoipites cryptoporus</i>	Porters Creek	Hatchetigbee	C
<i>Rhoipites latus</i>	Tallahatta	Zilpha	GCP
<i>Rhoipites</i> sp. 1	Naheola	Meridian	N
<i>Rhoipites</i> sp. 2	Tallahatta	Tallahatta	N
<i>Rhoipites</i> sp. 4	Naheola	Hatchetigbee	N
<i>Rhoipites</i> sp. 5	Zilpha	Zilpha	N
<i>Sandiegopollis</i> sp. 1	Hatchetigbee	Hatchetigbee	N
<i>Sequoiapollenites</i> spp.	Porters Creek	Tallahatta	G
<i>Siltaria-Cyrtaceapollenites</i> Complex	Naheola	Zilpha	G
<i>Siltaria</i> cf. <i>S. scabriextima</i> of Frederiksen 1980	Naheola	Tallahatta	GCP
<i>Sparganiaceapollenites</i> spp.	Naheola	Tallahatta	G
<i>Spinaepollis spinosa</i>	Naheola	Hatchetigbee	W
<i>Spinizonocolpites prominatus</i>	Tusahoma	Tallahatta	W
<i>Stereisporites granistereoides</i>	Porters Creek	Hatchetigbee	C
<i>Stereisporites stereoides</i>	Porters Creek	Tallahatta	C

Taxon	First appearance	Last appearance	Immigration/ speciation
<i>Symplocos? contracta</i>	Tallahatta	Tallahatta	GCP
<i>Symplocos? gemmata</i>	Tallahatta	Zilpha	GCP
<i>Symplocos? virginensis</i>	Tuscahoma	Tuscahoma	N.am
<i>Symplocos</i> sp. 2	Tuscahoma	Tuscahoma	N
<i>Tetracolporopollenites megadolium</i> type	Tuscahoma	Zilpha	GCP
<i>Tetracolporopollenites prolatus</i>	Tallahatta	Zilpha	GCP
<i>Thompsonipollis</i> cf. <i>T. expositus</i> of Frederiksen 1979	Tuscahoma	Tuscahoma	C
<i>Thompsonipollis magnificus</i>	Porters Creek	Tallahatta	C
<i>Toroisporites</i> spp.	Porters Creek	Hatchetigbee	G
<i>Tricolpites asper</i>	Porters Creek	Hatchetigbee	C
<i>Tricolpites crassus</i>	Tuscahoma	Tuscahoma	N.am
<i>Tricolpites hians</i>	Porters Creek	Zilpha	C
<i>Tricolpites reticulatus</i>	Hatchetigbee	Tallahatta	N.am
<i>Tricolpites</i> sp. 2	Hatchetigbee	Zilpha	N
<i>Tricolpites</i> sp. 3	Nanafalia	Tuscahoma	N
<i>Tricolpites</i> sp. 4	Tuscahoma	Zilpha	N
<i>Tricolpopollenites geranioides</i>	Nanafalia	Tuscahoma	N.am
<i>Tricolpopollenites</i> sp. 1	Meridian	Meridian	N
<i>Tricolporopollenites</i> sp. 1	Tuscahoma	Tuscahoma	N
<i>Tricolporopollenites</i> sp. 2	Naheola	Naheola	N
<i>Tricolporopollenites</i> sp. 3	Tuscahoma	Tuscahoma	N
<i>Tricolporopollenites</i> sp. 4	Naheola	Naheola	N
<i>Tricolporopollenites</i> sp. A of Tschudy 1973	Naheola	Meridian	GCP
Trilete spore, clavate	Hatchetigbee	Hatchetigbee	N
Trilete spore, reticulate	Hatchetigbee	Hatchetigbee	N
Trilete spore, verrucate	Tuscahoma	Tuscahoma	N
<i>Trivestibulopollenites</i> spp.	Porters Creek	Zilpha	G
<i>Trudopollis plenus</i>	Porters Creek	Tuscahoma	C
<i>Ulmipollenites krempii</i>	Porters Creek	Zilpha	C
<i>Ulmipollenites tricostatus</i>	Hatchetigbee	Hatchetigbee	C
<i>Ulmipollenites undulosus</i>	Hatchetigbee	Hatchetigbee	N.am
<i>Verrucatisporites</i> spp.	Porters Creek	Zilpha	G
<i>Wodehousia spinata</i>	Nanafalia	Nanafalia	C
<i>Zlivisporis novamexicanum</i>	Porters Creek	Hatchetigbee	C

first appearance on the GCP.

4. *In situ* speciations: these are form species that either have no recorded occurrences prior to their first appearances on the GCP, or have no previous published records and are counted as new taxa (see Chapter 4 for systematic descriptions). The taxa in the latter group are only tentatively counted as speciations, because (a) they are typically rare (see Chapter 4, and results below) and have little apparent biostratigraphic value, and so may not previously have been published even if they have been observed in other workers' samples, and (b) may have been missed in my own investigations of the published literature, which has necessarily only covered a fraction of what has previously been published.

The number of taxa in each of the above categories was tabulated, both for the dataset as a whole and for first appearances in each formation (excluding taxa that are limited to one formation, to limit sampling issues and noise [Foote and Raup, 1996; Olszewski and Patzkowsky, 2001b]).

7.3 Results

7.3.1 *Palynofloral diversity on the GCP and in Colombia*

Within-sample richness (observed, with individual based rarefaction)

When rarefied to 50 grains/sample (Fig. 7.1, upper row), both the GCP and Colombia show similar trends. Richness is ~ 15 taxa per sample in the Paleocene, increases to ~18 in the Early Eocene, and then rises to ~24 in the Middle Eocene. Within sample richness in the Middle Eocene is significantly higher than in previous time bins for both regions. Differences between the GCP and Colombia within each

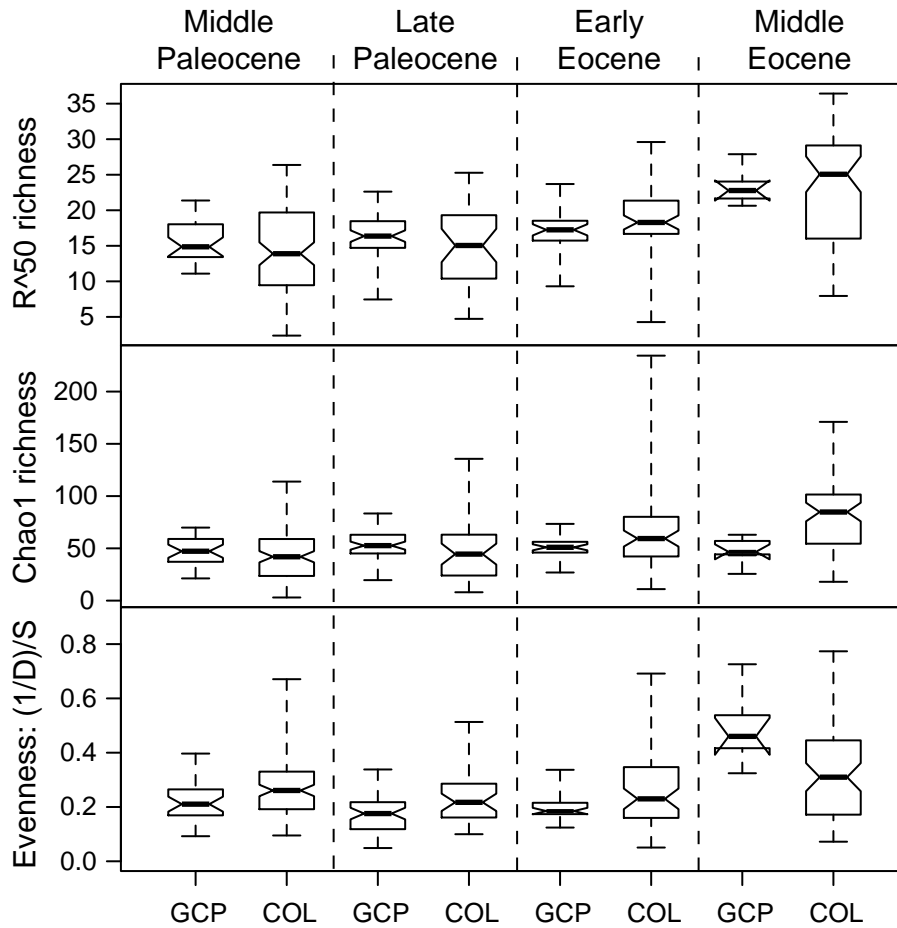


Figure 7.1. Box-and-whisker plots showing within-sample diversity (richness and evenness) information for the US Gulf Coastal Plain (GCP) and Colombia (COL), from the Middle Paleocene to the Middle Eocene. For each group of samples the thick horizontal line in the middle of the box shows the median value, the bottom and top of the box show the 25th and 75th percentiles, respectively, and the 'whiskers' show the most extreme values. Notches above and below the median show 95% confidence intervals. Upper row shows rarefied richness at 50 grains per sample counted; middle row shows estimated species richness using the Chao1 richness estimator; lower row shows Simpson's evenness metric (see text for details).

time bin are not significant.

Within-sample richness (estimated)

The GCP remains stable at ~50 taxa per sample from the Middle Paleocene to the Middle Eocene (Fig. 7.1, middle row). Estimated within-sample richness in Colombia is similar to the GCP during the Paleocene, but increases in the Eocene. By the Middle Eocene Colombian richness is at ~80 taxa per sample, which is significantly higher than in previous time bins, and significantly higher than on the GCP.

Within sample evenness

Evenness on the GCP remains stable until the Middle Eocene (Fig. 7.1, lower row), when it increases markedly (~0.2 to ~0.5). The Colombian evenness levels are similar to those on the GCP, but the increase in the Middle Eocene is much less marked (increase to ~0.3). The GCP Middle Eocene evenness is significantly higher than the Colombian Middle Eocene evenness.

Within-Age richness (observed, with sample based rarefaction)

Within-Age richness levels increase in both regions (Fig. 7.2A and B) during the study interval, with the Middle and Early Eocene richness being significantly higher than that of the Paleocene. None of the rarefaction curves fully saturate, demonstrating that both regions are undersampled. Richness is similar on the GCP and in Colombia (Fig. 7.3) during the Middle Paleocene, but from the Late Paleocene

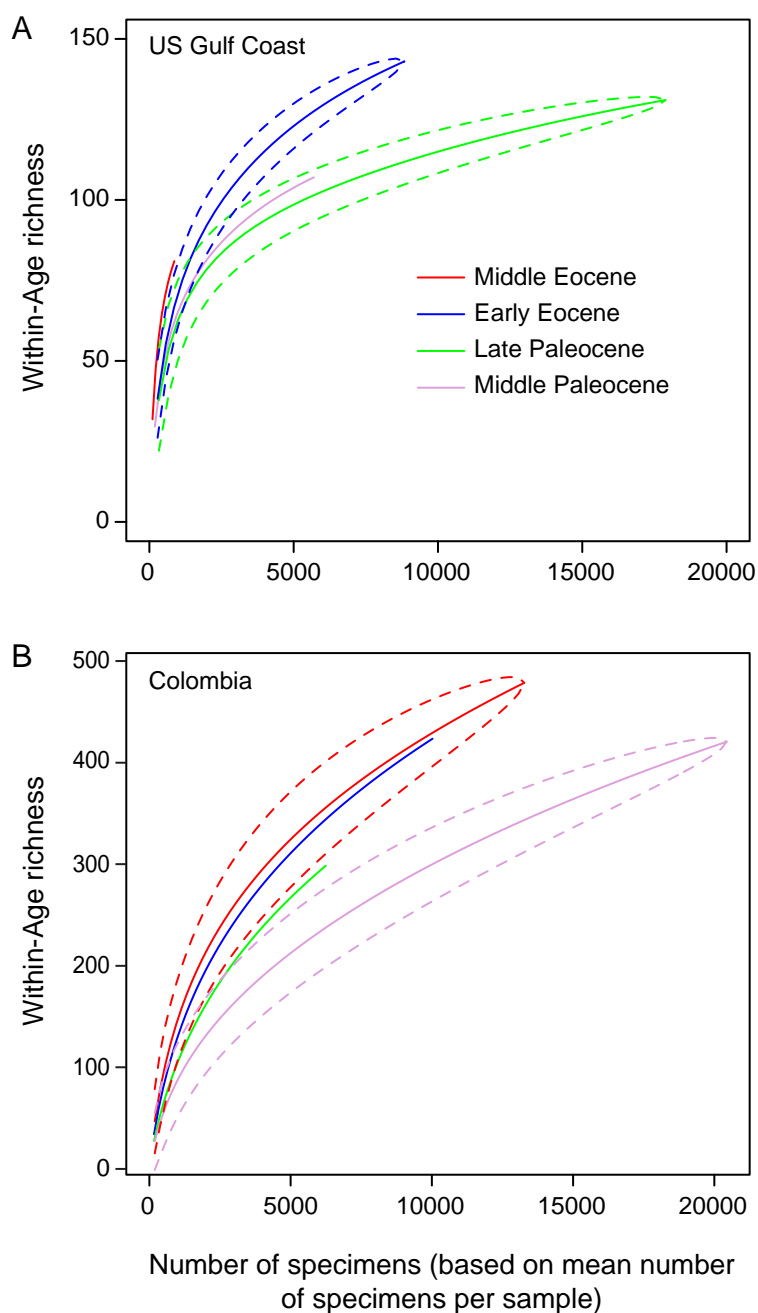


Figure 7.2. Sample-based rarefaction curves, showing within-Age richness for the US Gulf Coastal Plain (A) and Colombia (B). The y-axis shows the expected within-Age richness, and the x-axis shows the number of pooled samples. The x-axis has been rescaled to number of specimens, based on the mean number of specimens per sample for each curve (Gotelli and Colwell, 2001; Colwell et al., 2004; see also Chapter 5). Dashed lines about curves are 95% confidence intervals. Legend for (B) as in (A).

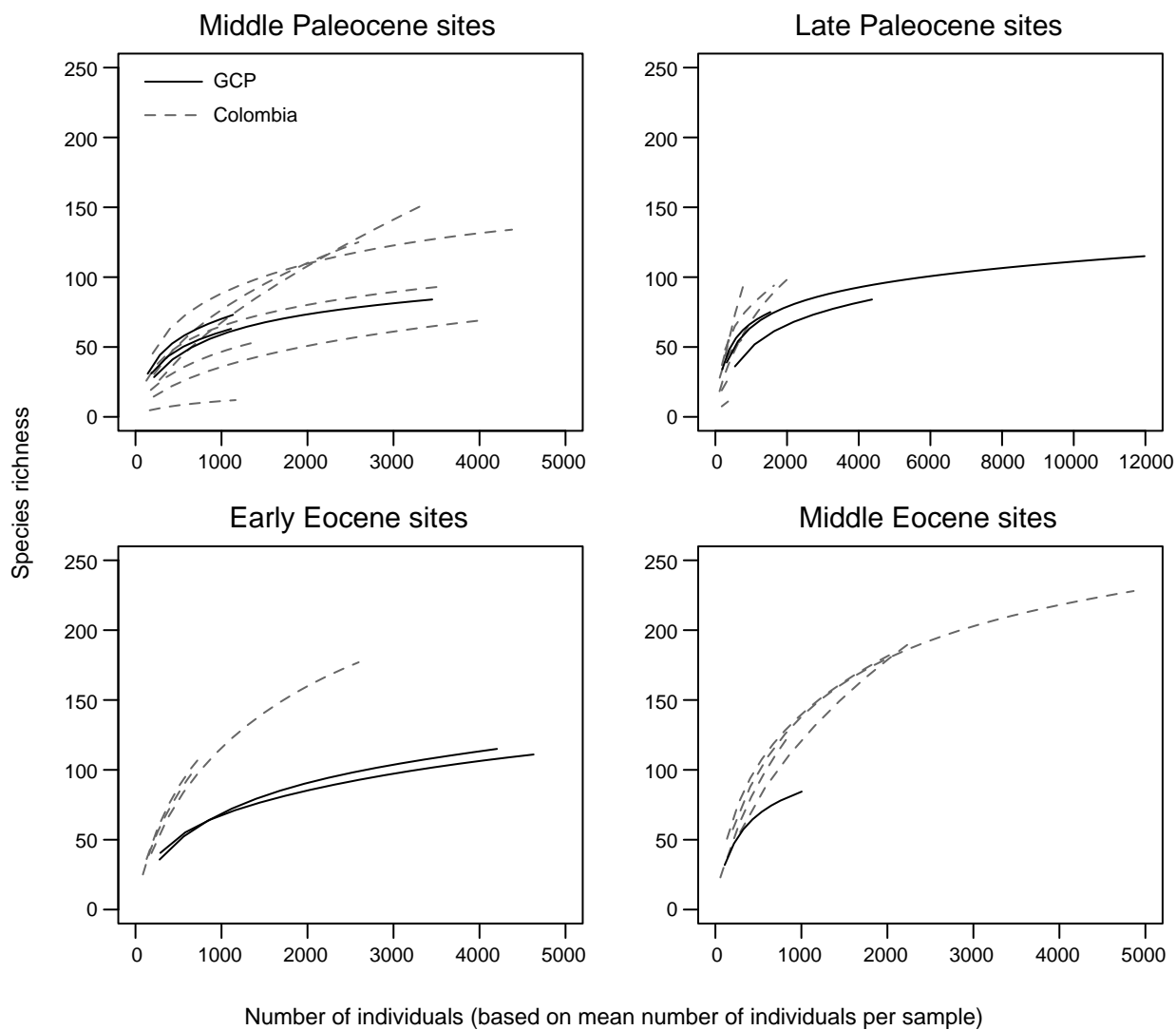


Figure 7.3. Sample-based rarefaction curves for each site (core or outcrop) within each time bin. Solid black lines = US Gulf Coastal Plain, and grey dashed lines = Colombia. Note the different scale on the x-axis of the Late Paleocene graph.

onwards richness levels in Colombia increase beyond that of the GCP. The higher richness levels for the entire Colombian region compared to the richness levels for individual sampling localities (Figs. 7.2 and 7.3) reveals the influence of the larger geographic area from which the Colombian data were derived, compared to that on the GCP (see also Chapter 6).

Within-Age richness (estimated)

For the GCP as a whole (Fig. 7.4A), there is no clear significant increase in estimated species richness through the study interval. The Late Paleocene curve saturates by 30 samples, suggesting that the estimate of ~155 taxa is robust to further sampling. Both the Middle Paleocene and Early Eocene curves may be approaching an asymptote, but further sampling is required to confirm whether estimated species richness in these time bins is significantly different to the Late Paleocene. The estimated species richness for the Middle Eocene is the lowest of the four time bins, but is also the least intensively sampled. The Colombian data (Fig. 7.4B) show an increase in estimated richness with each time bin. Only the Middle Paleocene curve appears to be saturating, at ~700 taxa with >100 samples pooled. At this level of sampling the Middle Eocene curve has a significantly higher estimated richness than the Middle Paleocene.

Comparing the two regions directly (by core/sampling locality; Fig. 7.5) provides less clearly interpretable results, as the Colombian curves occupy a range of values in each time bin. The GCP curves are more consistent in their trajectory. However, the GCP and Colombia are broadly comparable for the Paleocene, and the

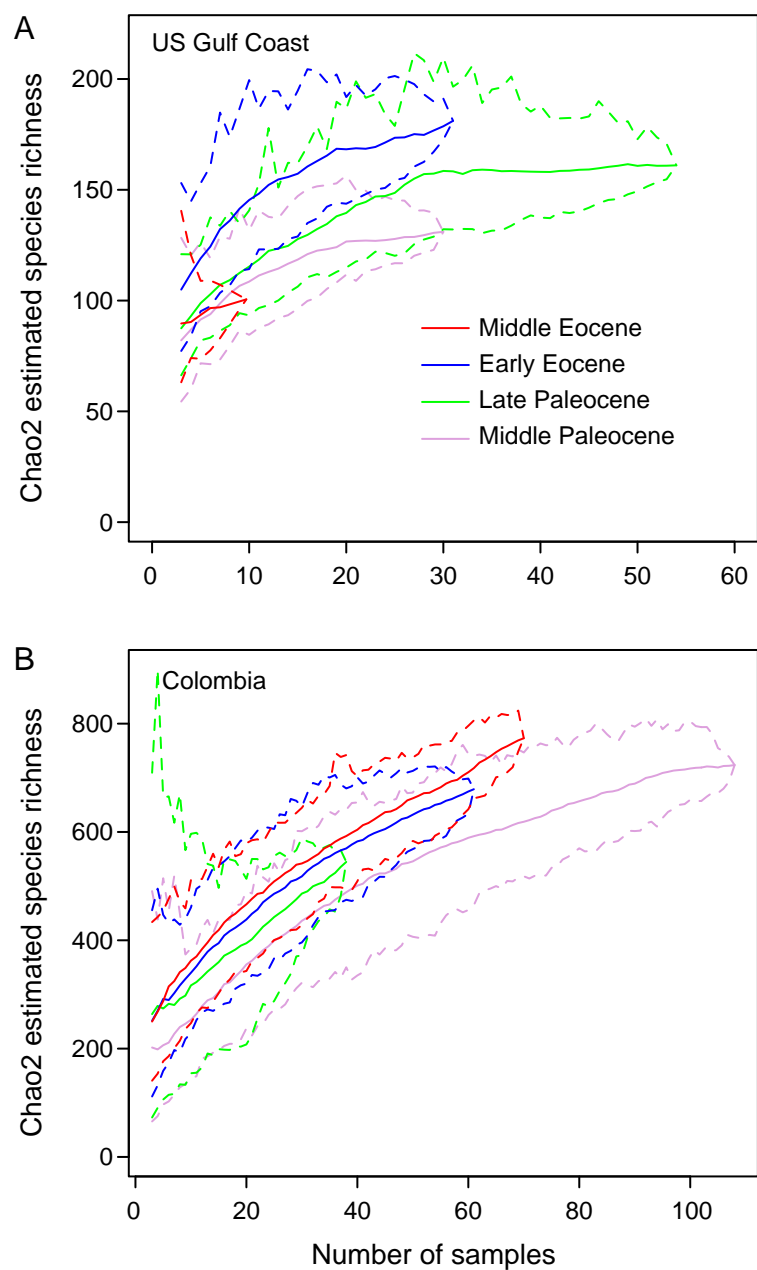


Figure 7.4. Chao2 estimated within-Age species richness curves for the US Gulf Coastal Plain (A) and Colombia (B). The x-axis shows the number of accumulated samples, and the y-axis shows the estimated species richness. Dashed lines about curves are 95% confidence intervals. Key for (B) as in (A).

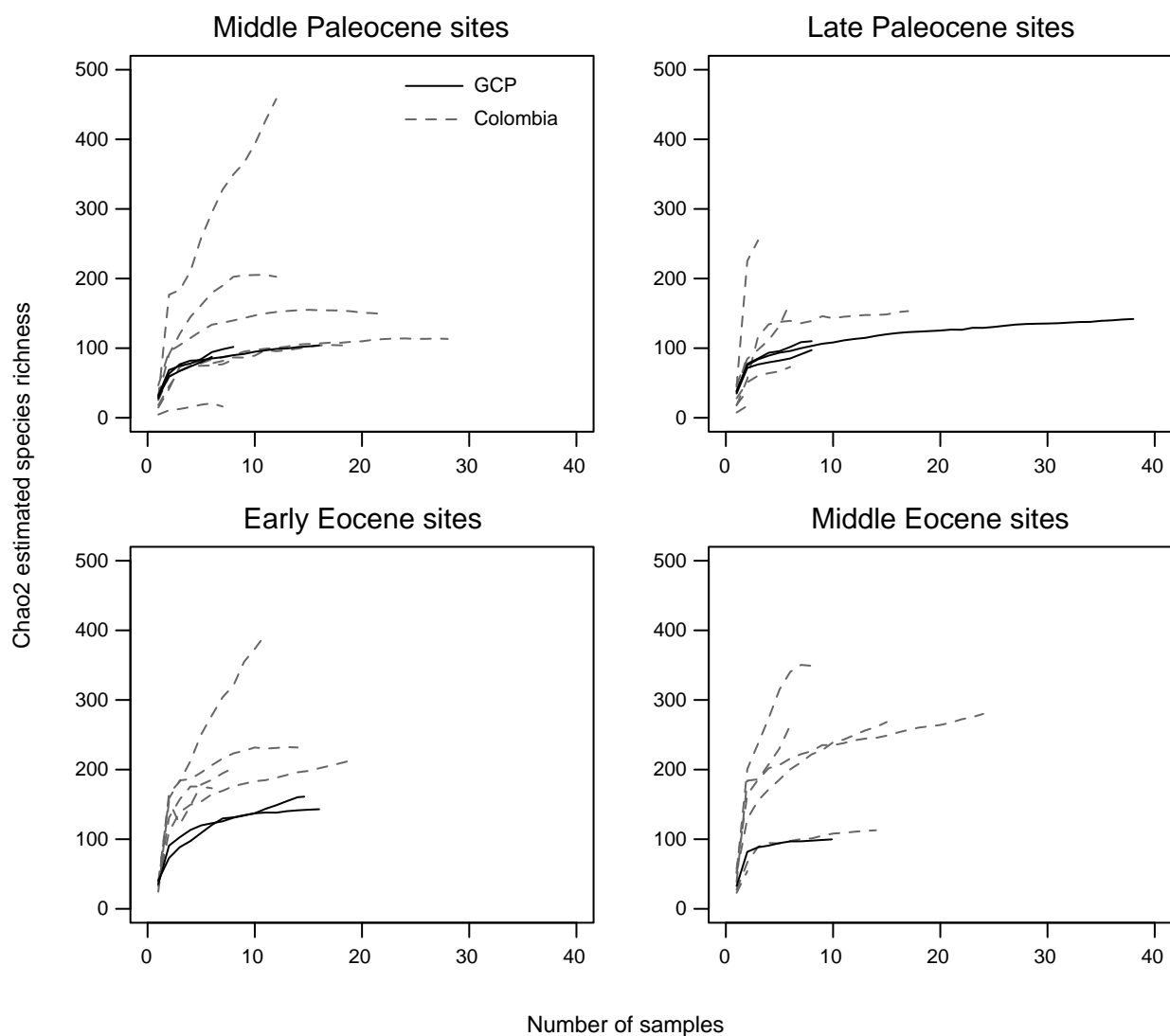


Figure 7.5. Chao2 estimated species richness curves for each site (core or outcrop) within each time bin. Solid black lines = US Gulf Coastal Plain, and grey dashed lines = Colombia.

Colombian floras increase above the GCP in the Early Eocene and Middle Eocene.

7.3.2 GCP compositional changes

NMDS

Ordinating the GCP (Fig. 7.6) data shows a gradual temporal gradient through time. There is a compositional shift from the Porters Creek to the Naheola formations, relative stability throughout the rest of the Paleocene (Naheola to Tuscahoma formations), and then larger shifts into the Early and Middle Eocene. The largest compositional breaks occur between the Tallahatta and Zilpha formations, and between those and the older formations. While the major temporal gradient is aligned with NMDS axis 1, the explanatory variable associated with NMDS axis 2 is unclear.

GCP turnover (first and last appearances)

Proportional first and last appearances (Fig. 7.7) remain at background levels throughout the study interval. The only increases beyond background levels occur within the Naheola Formation for first appearances, and within the Tallahatta Formation (Basic City Member) for last appearances. Given the proximity to the base and the top of the section, respectively, these departures from the null model are probably edge effects (Foote, 2000), rather than genuine examples of increased turnover.

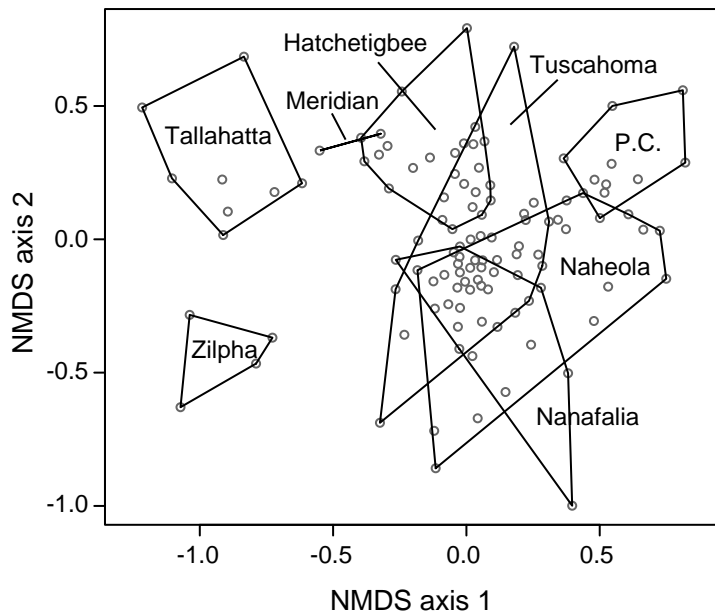


Figure 7.6. Non-metric multi-dimensional scaling (NMDS) plot of samples from the GCP. Grey circles are samples, and convex hulls are formations. P.C. = Porters Creek, Meridian = Meridian Sand Member of the Tallahatta Formation, Tallahatta = unnamed upper member of the Tallahatta Formation; see Figure 7 for stratigraphy.

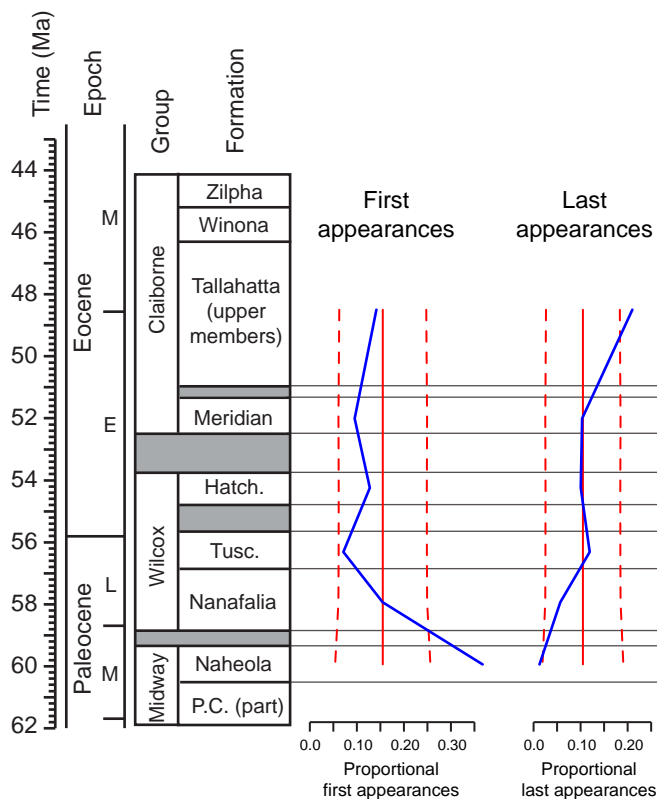


Figure 7.7. First and last appearance data (blue lines) for the Naheola to Tallahatta formations, expressed as proportions of standing richness (not shown). The red solid line shows expected first/last appearances given a constant level of turnover for the section. The dashed lines are 95% confidence intervals (see text for details).

7.3.3 *Immigration versus speciation on the GCP*

Tabulating all taxa (Fig. 7.8A) reveals that ~40% are either generalised types or were already present on the GCP, and are thus uninformative for the present question. Of the remainder, 61% are potential speciations and 39% are immigrations. A large percentage (64%) of the speciations are 'new' taxa; however, so many of these are rare and restricted in their distributions that removing unique taxa at the sample and formation levels (Figs. 7.8B and 7.8C respectively) greatly reduces the size of this group relative to the others. When formation uniques are removed (Fig 7.8C) 38% of the informative taxa (those that are not generalised types or already present) are speciations.

Excluding unique taxa at the formation level, and tabulating first appearances by formation (Fig. 7.9), reveals several major trends:

1. There is a gradual reduction in the number of first appearances of taxa that were already present on the GCP prior to the Middle Paleocene, and no more by the Hatchetigbee Formation.
2. Generalised types occupy 7 – 40% of first appearances.
3. Speciations (including 'new' taxa) typically occupy 25 – 50% of the remaining portion, except in the Tuscahoma and Tallahatta formations, in which speciations account for 75% and 100% of the remaining taxa, respectively (although in each case this group only comprises three first appearances, and there are very few or no immigration events). There is no obvious increase in the proportion of speciations during the Early Eocene warming phase.
4. In the Paleocene most immigrants are derived from elsewhere in North America,

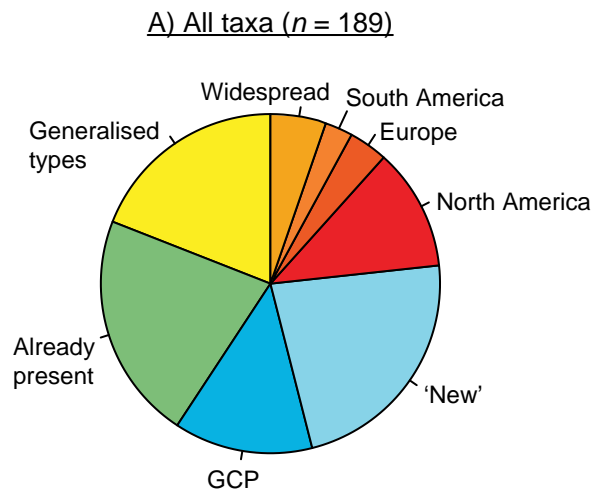
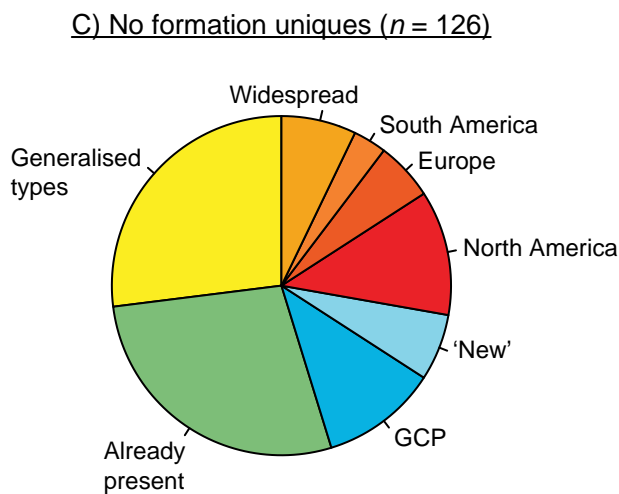
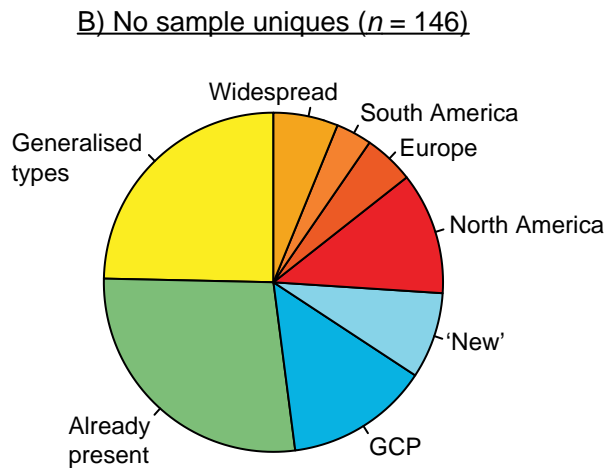


Figure 7.8. Speciation versus immigration for GCP taxa (all samples pooled). Blue segments represent taxa that are likely speciations, and red/orange segments represent taxa that are likely immigrants. (A) All taxa, (B) taxa that are limited to one sample removed and (C) taxa that are limited to one formation removed.



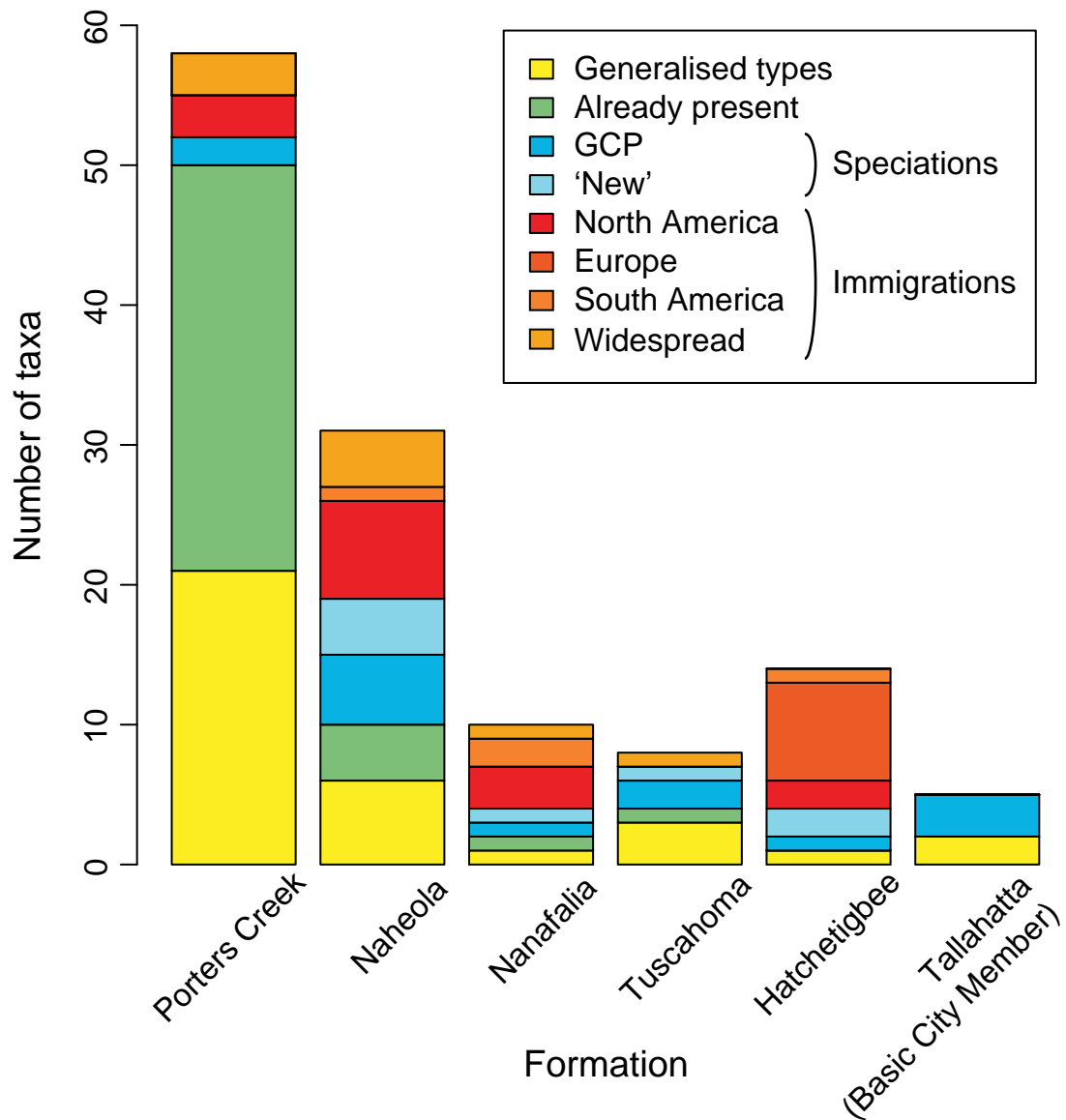


Figure 7.9. Speciation versus immigration for GCP taxa, tabulated by formation. Only taxa that occur in more than one formation are shown; there are no first appearances meeting this criterion in the Meridian Sand Member or Zilpha Formation.

with some coming from South America or being geographically widespread. A major change in the Early Eocene Hatchetigbee Formation is an influx of immigrants from Europe.

7.4 Discussion and conclusions

7.4.1 GCP versus Neotropical diversity during the early Palaeogene

These results show that species richness was similar on the GCP and in Colombia during the Paleocene. However, while species richness in Colombia increased in the Early and Middle Eocene (Jaramillo et al., 2006), richness on the GCP remained relatively stable throughout the study interval. The GCP palynoflora in the Middle Eocene is more diverse in the sense that it is more even at the within-sample level, which causes an apparent increase in rarefied within-sample species richness. Extrapolated within-sample species richness remains stable into the Middle Eocene, however. Rarefied within-Age species richness did increase between the Paleocene and Eocene on the GCP, but this increase is small compared to that in Colombia.

Contrary to patterns in Colombia (Jaramillo, 2002), *in situ* speciation on the GCP remained at uniform levels throughout the early Palaeogene warming, and most first appearances were from intra- and intercontinental immigrations. Throughout the study interval, first appearances largely acted to replace extinctions, and maintained GCP richness at a stable level. The uniformly low levels of turnover are backed up by the NMDS analysis, which shows a more or less steady temporal gradient of compositional change over time.

Only a minority of immigration events were from South America, confirming

the lack of dispersal potential from the neotropics (Jaramillo and Dilcher, 2001; Harrington and Jaramillo, 2007). A major shift occurs in the Hatchetigbee Formation, with an influx of immigrant taxa from Europe (Frederiksen, 1994b; 1998; Harrington, 2003b). Many of these have first appearances on the GCP that coincide with rapid warming during the PETM (Harrington, 2001; 2003b; Harrington and Jaramillo, 2007). Although the same warming episode stimulated speciation in the neotropics (Jaramillo et al., 2010), it does not appear to have done so on the GCP.

The LDG between the Neotropics and southern North America (~30°N) was therefore suppressed, and possibly non-existent, during the Paleocene. In the Early Eocene rapid diversification in the Neotropics, muted diversification on the GCP, and a lack of northward dispersal from the Neotropics into North America, greatly steepened the northern hemisphere LDG.

7.4.2 The influence of temperature on paratropical speciation, and implications for the form and maintenance of the LDG

These results do not support a primary role for temperature in controlling speciation rate. Species richness, proportional first appearances and the proportion or number of speciation events on the GCP showed little or no sign of increasing with the Early Eocene warming. These findings in no way contradict those studies that have found a positive correlation between ambient temperature and the rate of molecular evolution in modern organisms (Wright et al., 2003; Davies et al., 2004; Gillooly et al., 2005; Allen et al., 2006; Wright et al., 2006; Gillman et al., 2009). They do, however, suggest that such a relationship does not scale up to stimulating

speciation over longer timescales.

These results have important implications for how we can understand, and ultimately model, the form and maintenance of the LDG through time and space. That paratropical warming did not increase speciation rates suggests that when extra-tropical areas are warmed to megathermal levels, they do not become active areas of speciation (that is, the effective area for enhanced speciation relative to higher latitudes does not increase). Regional richness may increase with range shifts out of the tropics if suitable migration routes are available, and our results cannot address whether speciation within these lineages may occur in their expanded ranges. Extra-tropical megathermal areas may also be important biodiversity stores for species range extensions into higher latitudes; at least some of the immigrations into the North American Western Interior during the Late Paleocene-Early Eocene warming are probably derived from the GCP (Wing et al., 2005). My results do suggest that warming *per se* does not turn extra-tropical regions into cradles of evolution, however, and that during globally warm phases elevated low latitude speciation rates are limited to the tropics proper.

The lack of an increase in speciation with temperature in the paratropics also suggests that Early Eocene Neotropical diversification (Jaramillo et al., 2006) was not driven by regional temperature change directly influencing speciation rates. This can only have been the case if, (a) the relationship between temperature change, molecular evolution rate and speciation rate operates differently in the tropics compared to extra-tropical latitudes, or (b) regional temperatures near the equator reached some critical temperature threshold, which was not attained as far away as

southern North America. The former scenario is hard to envisage unless some other abiotic or biotic factors that are present in the tropics but not elsewhere interact with temperature to drive increased speciation. The latter scenario would imply that increased tropical temperatures could only have been important for maintaining the LDG during the warmest interval of the Cenozoic (Zachos et al., 2001; Zachos et al., 2008), and not since.

The early Palaeogene GCP has previously been portrayed as an immigration limited system, which relied on intra- and intercontinental immigrations to increase species richness (Frederiksen, 1994b; Harrington and Jaramillo, 2007). My results entirely support this view of the paratropical forests on the GCP. The wider implications of this are that when temperature regimes reached tropical levels in extra-tropical regions, the speciation rate did not increase to the levels experienced in the equatorial tropics. This not only calls into question the direct influence of temperature on speciation rate, but also shows that latitudinal controls on the form of the LDG are non-linear and complex. The challenge now for workers modelling the LDG is to incorporate speciation, extinction, and dispersal gradients as variables that are dynamic in time and space, and to understand the environmental and biotic controls on those gradients.

CHAPTER 8: CONCLUSIONS

8.1 Restatement of thesis aims

Using a new, high-resolution sporomorph dataset, the aims of this thesis were:

1. To fully document the early Palaeogene Gulf Coastal Plain (GCP) sporomorph assemblage, and to describe any new taxa that are found.
2. To test how a fully comprehensive sampling approach (e.g. counting all taxa in a sampling unit) alters our understanding of past biodiversity compared to biostratigraphic data collection.
3. To test the influence of temperature regime on the spatial distribution of biodiversity in extra-tropical floras, in relation to modern tropical and extra-tropical biomes.
4. To test the relationship between MAT and diversity, speciation, extirpation and dispersal.

8.2 Major findings of thesis

I have counted 151 samples from the Middle Paleocene to Middle Eocene of the GCP, and assembled a dataset comprising 41831 counted specimens and 214 sporomorph morphotypes. Fifty-nine of these morphotypes were not found in the published literature and have been described and informally named in Chapter 4. All other taxa are discussed in Appendix 1, with brief synonymy lists and occurrence details given. The whole dataset is illustrated in the Plates section.

In a preliminary investigation I studied in detail eight Late Paleocene samples

from the Red Hills Mine of Mississippi (Chapter 5). In addition to providing detail on the GCP palynofloral composition and lithological influences, the findings from this study show that GCP diversity previously tabulated from biostratigraphic data has been underestimated. This (a) provides the rationale for constructing a new dataset to study biodiversity patterns throughout the early Palaeogene, and (b) justifies the sampling method employed in this project, whereby all taxa are counted and not just those with some biostratigraphic utility.

Spatially, it was not possible to associate the Late Paleocene GCP vegetation more closely with either tropical or extra-tropical modern biomes (using the Holocene pollen record as a proxy; Chapter 6). This was because of the combination of rate and scale-dependency in the distance decay of compositional similarity of those biomes: the tropical biome shows a higher rate of compositional decay with geographic distance than the extra-tropical biomes, but is also more compositionally similar at smaller inter-site distances. These findings do, however, support the presence of a modern latitudinal gradient in spatial turnover, and show the potential of the sporomorph record for studying spatial biotic patterns. The importance of compositional heterogeneity for maintaining regional species richness across the GCP was also demonstrated by these results.

Temporally, there was no evidence that during the Late Paleocene-Early Eocene warming the GCP paratropics took on a 'tropical' character in terms of their diversity and turnover trajectory (Chapter 7). Whereas Neotropical floras diversified during this global warming trend and attained their highest species richness of the Cenozoic (Jaramillo et al., 2006), species richness remained stable

on the GCP throughout this interval, as did first and last appearance levels. Within the first appearances there is no sign that speciation increased in concert with the warming trend; the only obvious correlation with warming appears to be an influx of European immigrant taxa during or near the PETM (Harrington, 2001; 2003b). Range expansions from the Neotropics also show no signs of increasing in frequency with warming, both confirming previous studies that have found a low compositional similarity between the GCP and Colombia at this time (Jaramillo and Dilcher, 2001; Harrington and Jaramillo, 2007), and demonstrating the efficacy of the intercontinental seaway as a barrier to plant dispersal.

These results have several wider implications for the form of the latitudinal diversity gradient (LDG) through time, and for macroecological and macroevolutionary studies in general. First, the lack of an increase in the output of new species during the Early Eocene warm period does not support the hypothesis that increased rates of molecular evolution in warmer climates drives increased speciation rates in lower latitude areas. In itself this result adds to the debate on the importance of climate in controlling patterns of biodiversity (Janis, 1993; Alroy et al., 2000; Wing and Harrington, 2001): regional richness may be shaped by climatic change by allowing dispersal into new areas (Roy, 2001), but the input of new taxa into a species pool by speciation does not obviously increase by temperature change alone.

In the context of the LDG, this means that the area of enhanced low latitude speciation is not expected to increase during globally warm periods. Tropical diversification, and thus the number of taxa with tropical adaptations (Wiens and

Donoghue, 2004), may increase in rate in the equatorial tropics (Jaramillo et al., 2006), but enhanced speciation relative to higher latitudes does not spread out into paratropical areas in an easily predictable manor. Information such as this can form the basis of more accurate numerical models of the LDG that incorporate a historical perspective (Goldberg et al., 2005; Roy and Goldberg, 2007), and ultimately spatially explicit models of global diversification through changing global climatic regimes.

APPENDIX 1: SUPPLEMENTARY SYSTEMATICS

This section provides systematic information for taxa that have been described in the published literature. For these taxa I have followed the existing taxonomy and have avoided transferring species between genera, or emending existing descriptions. Where taxa have previously been assigned to both form genera and extant genera I have generally maintained the use of form genera, because of the uncertainty of assigning fossil sporomorphs to modern taxa (Traverse, 1988). However, where the morphology of the modern pollen is unambiguously tied to one genus, or when a Palaeogene fossil record is known to exist for an extant genus (i.e. through leaf macrofossils), the use of extant taxa is justified (e.g. Frederiksen, 1980a, 1988; Nichols, 2010). Taxa that were only assigned an informal name by previous authors are referred to by the same name in this dataset, but are denoted by the use of quotation marks and a reference to the original author (i.e. “*Retitrescolpites* sp. 1” of Frederiksen 1983). As with the descriptions of new taxa in Chapter 4, the following information is arranged by major morphological group, and then alphabetically by genus and species. The synonymy list for each taxon focuses on taxonomic changes, and prior North American (and especially US Gulf Coast) occurrences. Where botanical affinities have been suggested in the literature these have been included, using the Angiosperm Phylogeny Group (APG) III classification system (APG III, 2009) for angiosperms, and that of Smith et al. (2006) for ferns.

MONOLETE ISOSPORES

Genus *Laevigatosporites* Ibrahim 1933

Type species. *Laevigatosporites vulgaris* (Ibrahim in Potonié, Ibrahim & Loose 1932) Ibrahim 1933.

Remarks. This genus includes bean-shaped monolete spores with thin, psilate exine. The monolete scar is straight and simple, and typically extends over half the length of the grain. *Laevigatosporites* is differentiated from other monolete spores by its smooth, thin exine.

Laevigatosporites haardtii (Potonié & Venitz 1934) Thomson & Pflug 1953

Plate 1, figure 1

Sporites haardtii Potonié and Venitz, 1934, p. 13, pl. 1, fig. 13.

Laevigatosporites haardtii (Potonié & Venitz) Thomson and Pflug, 1953, p. 59, pl. 3, figs. 27-38; Srivastava 1972, p. 232, pl. 5, fig. 9-10; Frederiksen, 1980a, p. 28, pl. 1, fig. 1; Jardine and Harrington, 2008, pl. 1, fig. 1.

Laevigatosporites spp. Elsik, 1968a, p. 290, pl. 6, fig. 4-7; pl. 7, fig. 1.

Laevigatosporites spp. Pocknall and Nichols, 1996, p. 10-11, pl. 1, fig. 14.

Dimensions. Length 31 – 61 μm , mean 44 μm ; height 19 – 41 μm , mean 27 μm (five specimens measured). Thomson and Pflug (1953) gave a length range of 25 – 70 μm .

Remarks. *Laevigatosporites haardtii* includes bean-shaped to slightly ovoid monolete spores with a smooth exine. In my material the laesurae are simple and are 1/2 to 2/3 the length of the spore. The more ovoid forms may represent *Laevigatosporites ovatus* Wilson & Webster 1946, but here I follow Srivastava (1972) in not discriminating between these form species, given the large degree of overlap in shape and size between them. *Laevigatosporites adiscordatus* Krutzsch 1959 has faint infratectal reticulations, and *Laevigatosporites discordatus* Pflug in Thomson & Pflug 1953 has thick lips around the laesurae (Srivastava, 1971); *Laevigatosporites haardtii* lacks both of these features.

Botanical affinity. Frederiksen (1980a) suggested that *Laevigatosporites haardtii* could have been produced by species belonging to the fern families Aspidiaceae,

Aspleniaceae, Blechnaceae, Gleicheniaceae, Lomariopsidaceae, Polypodiaceae or Pteridaceae.

Occurrence. Present in every sample, reaching a maximum relative abundance of 29.5%. This form species is geographically widespread in the Cretaceous and Cenozoic (Srivastava, 1972; Frederiksen, 1980a).

Genus *Microfoveolatosporis* Krutzsch 1959 emend. Potonié 1966

Type species. *Microfoveolatosporis pseudodentatus* Krutzsch 1959.

Remarks. *Microfoveolatosporis* represents bean-shaped monolete spores with punctate/foveolate to reticulate ornamentation. Muri thickness is at least half the lumina diameter, excluding reticulate monolete spores with thin muri. The depressions are shallow and rounded, and can give the exine an undulated appearance in cross-section. The dehiscence mark is straight. This form genus is therefore easily distinguished from *Laevigatosporites* Ibrahim 1933 by the presence of an exine sculpture in *Microfoveolatosporis*.

Microfoveolatosporis pseudodentatus Krutzsch 1959

Plate 1, figure 2

Microfoveolatosporis pseudodentatus Krutzsch, 1959a, p. 212, pl. 41, figs. 463-466; Elsik, 1968a, p. 290, pl. 7, fig. 5; Frederiksen, 1980a, p. 29, pl. 1, fig. 4; Jardine and Harrington, 2008, pl. 1, fig. 2.

Microfoveolatosporis sp. Frederiksen, 1980b, p. 148, 150; pl. 1, fig. 1.

Dimensions. Length 29 – 56 μm , mean 44 μm ; height 21 – 30 μm , mean 25 μm (six specimens measured). Krutzsch (1959a) gave a length range of 65 – 80 μm for this

form-species. Elsik (1968a) recorded specimens from the Late Paleocene of Texas that fall within the size range of Krutzsch (1959a), whereas Frederiksen (1980b) described smaller specimens from the Paleocene of South Carolina that match better with my measurements.

Remarks. *Microfoveolatosporis pseudodentatus* contains punctate, monolete spores.

Over some parts of the spore surface the lumina may cluster together to form a reticulum, but this is only local variation on an otherwise punctate design.

Microfoveolatosporis pseudodentatus is similar in size, shape and dehiscence characteristics to *Laevigatosporites haardtii* (Potonié & Venitz 1934) Thomson & Pflug 1953, although this latter species has a thinner, psilate exine. Although my specimens fall below the size range given by Krutzsch (1959a), they match his description of this species in every other respect.

Botanical affinity. Frederiksen (1980a) listed Psilotaceae and Schizaeaceae as possible parent families.

Occurrence. Occurred in relative abundances of <6% in 58/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and the Calvert Bluff Formation in Texas. This species ranges into the Vicksburg Group (Lower Oligocene) on the US Gulf Coast (Frederiksen, 1980a).

Genus *Polypodiisporonites* Potonié 1931

Type species. *Polypodiisporonites favus* Potonié 1931.

Remarks. This form genus includes verrucate monolete spores with a bean-shaped amb. The verrucae may be arranged densely enough for a true negative reticulum to develop. The spore wall appears undulating in cross-section due to the presence of the verrucae.

Polypodiisporonites spp.

Plate 1, figure 3

Reticuloidosporites sp. Jardine and Harrington, 2008, pl. 1, fig. 3.

Lygodium sp. Jardine and Harrington, 2008, pl. 1, fig. 7.

Dimensions. Length 42.5 μm ; height 25 μm (one specimen measured).

Remarks. *Polypodiisporonites* spp. includes verrucate monolete spores. Elsik (1968a) recorded several species of *Polypodiisporonites* (= *Verrucatosporites* according to Frederiksen (1980a)) from the Late Paleocene of Texas, mainly differentiated by the size, shape and arrangement of the verrucae. Due to the rarity and lack of stratigraphic usefulness of these forms in my material, I have not attempted to differentiate my specimens to form-species level. More coarsely verrucate forms occur in the Claiborne and Jackson Groups of the US Gulf Coast (Fairchild and Elsik, 1969; Tschudy, 1973a; Frederiksen, 1980a), but were not observed in my samples.

Botanical affinity. Probably Polypodiaceae (Tschudy, 1973a; Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <1% in 20/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. Similar forms have been recorded from the Late Paleocene of Texas (Elsik, 1968a), and range through to at least the Late Eocene Jackson Group of Mississippi and Alabama (Frederiksen, 1980a).

Genus *Reticuloidosporites* Pflug in Thomson & Pflug 1953

Type species. *Reticuloidosporites dentatus* Pflug in Thomson & Pflug 1953.

Remarks. This form-genus describes bean-shaped monolete spores with a positive reticulate sculpture. It is therefore distinguished from *Microfoveolatosporis* Krutzsch

1959 which is foveo-reticulate and does not include densely reticulate forms, and *Polypodiisporonites* spp. which is verrucate and often displays a negative reticulum.

Reticuloidosporites spp.

Plate 1, figure 4

Dimensions. Length 34 μm , height 24 μm (one specimen measured).

Remarks. I have assigned monolete spores with a predominantly reticulate exine to *Reticuloidosporites* spp. The lumina are 1-3 μm in diameter. As with *Microfoveolatosporis pseudodentatus* Krutzsch 1959 the lumina are irregularly distributed, and areas of the exine are foveolate rather than reticulate (see illustrated specimens of *Reticuloidosporites pseudomurii* Elsik, 1968a, pl. 7, fig. 2; and in Pocknall and Nichols, 1996, pl. 1, fig. 15-16). Krutzsch (1959a) included both positively and negatively (i.e. densely verrucate) reticulate forms in *Reticuloidosporites*. Here I have followed Elsik (1968a) in only including spores with a positive reticulum, and have assigned verrucate forms to *Polypodiisporonites*.

Reticuloidosporites spp. was rare and has little apparent stratigraphic value, and so I have not attempted to assign specimens to individual form-species. Some specimens may be conspecific with *Reticuloidosporites pseudomurii*.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <2% in 46/151 samples, from base of the Porters Creek Formation to the lower part of the Tallahatta Formation on the eastern Gulf Coast, and the Calvert Bluff Formation in Texas.

TRILETE ISOSPORES

Genus *Appendicisporites* Weyland & Krieger 1953

Type species. *Appendicisporites tricuspидatus* Weyland & Greifeld in Weyland & Kreiger 1953.

Remarks. *Appendicisporites* represents triangular trilete spores, which are distinct from other trilete spores in having appendices formed from thickened exine on the equatorial angles. The exine is ornamented with ridges that run either parallel to the sides of the spore, or intersect the sides at a low angle. The proximal and distal ribs may or may not be parallel. *Cicatricosisporites* also has a ribbed exine; however this form genus lacks appendices on the equatorial angles.

Appendicisporites spp.

Plate 1, figure 5

Appendicisporites sp. Jardine and Harrington, 2008, pl. 1, fig. 4.

Dimensions. Equatorial diameter 33 – 46 μm , mean 39 μm (three specimens measured)

Remarks. The main morphological details of specimens recorded as *Appendicisporites* spp. have been mentioned in the genus remarks. The appendices extend 3 to 10 μm beyond the outer edge of the spore. The ridges run nearly parallel to the spore sides, and in contrast to *Appendicisporites crenimurus* Srivastava 1972 and *Appendicisporites dentimarginatus* Brenner 1963 have smooth crests.

Botanical affinity. Schizaeaceae (Srivastava, 1972).

Occurrences. *Appendicisporites* spp. was found as singletons in 3/151 samples, in the Porters Creek and Tusahoma formations. It was not recorded in Texas. Other morphotypes of this form genus have been found in the Paleocene of the Gulf Coast

and South Carolina (Fairchild and Elsik, 1969; Srivastava, 1972; Frederiksen, 1980b).

Genus *Baculatisporites* Pflug & Thomson in Thomson & Pflug 1953 emend. Krutzsch
1967

Type species. *Baculatisporites primarius* (Wolff 1934) Pflug & Thomson in Thomson & Pflug 1953.

Remarks. *Baculatisporites* includes trilete spores with subcircular amb. The laesurae reach the equator and the exine is thin. The exine is ornamented with widely spaced baculae; this feature separates *Baculatisporites* from other trilete spores.

Baculatisporites primarius (Wolff 1934) Pflug & Thomson in Thomson & Pflug 1953
Plate 1, figures 6-7

Sporites primarius Wolff, 1934, p. 66, pl. 5, fig. 8.

Baculatisporites primarius (Wolff) Pflug and Thomson in Thomson and Pflug, 1953, p. 56, pl. 2, figs. 49-53.

Osmunda primaria (Wolff) Frederiksen, 1980a, p. 31-32, pl.2, fig. 10.

Dimensions. Equatorial diameter 27 – 36 μm , mean 33 μm (four specimens measured). Wolff (1934) gave a range of 43 – 47 μm for the protologue specimens.

Remarks. The major distinguishing features of this species have been outlined in the genus remarks. My specimens match closely with the description given by Wolff (1934), having a thin exine, a subcircular amb, a thin trilete mark, and evenly spaced, short baculae that give the spore a battlement-like outline. Specimens illustrated by Pocknall and Nichols (1996) as *Baculatisporites* sp. from the Late Paleocene of the Western Interior have coarser ornamentation than my specimens.

Botanical affinity. Osmundaceae. Frederiksen (1980a) felt sufficiently confident of this species' affinities to transfer it to the extant genus *Osmunda* Linneaus.

However, given the presence of similar ornamentation in other extant genera of the Osmundaceae (see Jansonius and Hills 1976, card 219), I have retained the usage of *Baculatisporites*.

Occurrence. Occurred in relative abundances of <3% in 53/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. On the Gulf Coast this taxon is known to range up into the Late Eocene Yazoo Clay (Frederiksen, 1980a).

Genus *Bullasporis* Krutzsch 1959

Type species. *Bullasporis bullis* Krutzsch 1959.

Remarks. Krutzsch (1959a) erected *Bullasporis* to include trilete spores with one or more bubble-like outgrowths attached to the spore wall. These differ from verrucate trilete spores in having large bubble-like, rather than wart-like, sculptural elements.

Bullasporis spp.

Plate 1, figures 8-9

Bullasporis sp. Frederiksen, 1980a, p. 32, pl. 2, figs. 11-12.

Dimensions. Equatorial diameter 16 – 34 μm (two specimens measured).

Remarks. I have assigned to *Bullasporis* spp. trilete spores having bullae, 4 – 13 μm in diameter and 2 – 4 μm high, covering the distal face and equator. The proximal face is psilate, the amb in convex-triangular, and the trilete mark is fine and extends almost to the equator. The exine is ~1 μm thick. My specimens are therefore similar to

those illustrated by Frederiksen (1980a) except in terms of size, as Frederiksen's two specimens were larger at 48 and 57 μm .

Botanical affinity. Unknown.

Occurrence. Five specimens of *Bullasporis* spp. were observed; four were recorded in the Hatchetigbee Formation, and one in the Nanafalia Formation. Similar forms were recorded by Frederiksen (1980a) in the Late Eocene Moodys Branch Formation and Yazoo Clay in Mississippi.

Genus *Camarozonosporites* Pant 1954 ex Potonié 1956 emend. Klaus 1960

Remarks. See Chapter 4 for genus remarks and type species.

Camarozonosporites grootii Srivastava 1972

Plate 1, figures 10-11

cf. *Hamulatisporis amplus* Stanley 1965. Elsik, 1968a, p. 306, pl. 11, fig. 4-7.

Camarozonosporites grootii Srivastava, 1972, p. 226 – 227, pl. 3, fig. 3 – 5.

Dimensions. Equatorial diameter 41 - 46 μm , mean 44 μm (four specimens measured). Srivastava (1972) gave a range of 37 – 53 μm for the protologue specimens.

Remarks. *Camarazonosporites grootii* describes large, trilete spores, with long, thin laesurae, and widely spaced, tortuous rugulae on the distal face. My specimens correspond well with the description given by Srivastava (1972). *Camarozonosporites heskamensis* (Pflanzl) Krutzsch 1959 is smaller and has a finer distal ornamentation. *Camarozonosporites* sp.1 is larger (60 μm equatorial diameter), and has narrower rugulae and lumina.

Botanical affinity. Lycopodiaceae (Srivastava, 1972).

Occurrences. Occurred in relative abundances of <3% in 31/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Camarazonosporites heskamensis (Pflanzl 1955) Krutzsch 1959

Plate 1, figure 12

Cingulatisporites heskamensis Pflanzl in Mürriger and Pflanzl, 1955, p. 87, pl. 5, fig. 1-3.

Camarozonosporites heskamensis (Pflanzl) Krutzsch, 1959a, p. 187-188, pl. 38, fig. 413-421.

Lycopodium heskamensis (Pflanzl) Frederiksen, 1980a, p. 33, pl. 3, fig. 12-13.

Dimensions. Equatorial diameter 26 – 31 μm , mean 29 μm (five specimens measured).

Remarks. *Camarozonosporites heskamensis* has a finely rugulate distal face, a psilate proximal face, and distinct inter-radial crassitudes. The amb is subcircular in shape. This species is distinct from *Lycopodium hamulatum* (Krutzsch 1959) Frederiksen 1980, which has an uninterrupted cingulum rather than inter-radial crassitudes. It differs from *Camarozonosporites grootii* Srivastava 1972 in being smaller, having a shorter and more clearly defined trilete mark, and a finer distal ornamentation.

Botanical affinity. *Lycopodium* (Lycopodiaceae). Frederiksen (1980a) noted the similarity to *Lycopodium cernuum* Linnaeus.

Occurrence. Occurred in relative abundances of <3% in 12/151 samples, from the Tusahoma to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon is known to range up into the Early Oligocene Vicksburg Group in Mississippi and Alabama (Frederiksen, 1980a).

Genus *Cicatricosisporites* Potonié & Gelletich 1933

Type species. *Cicatricosisporites dorogensis* Potonié & Gelletich 1933.

Remarks. This form genus describes trilete spores with a striate exine. The striae are usually parallel but occasionally anastomosing, and lie at an angle to the equator. The tops and edges of the striae may be smooth, undulating or foveolate. *Cicatricosisporites* differs from *Appendicisporites* Weyland & Krieger 1953 in lacking appendices on the equatorial angles.

Cicatricosisporites dorogensis Potonié & Gelletich 1933

Plate 1, figure 14

Cicatricosisporites dorogensis Potonié and Gelletich, 1933, p. 522, pl. 1, figs. 1-5; Elsik, 1968a, p. 306-307, pl. 12, fig. 9; pl. 13; fig. 1-5, 7; Srivastava, 1972, p. 227, pl. 3, fig. 6-7; pl. 4, fig. 1-11; Frederiksen, 1980a, p. 32, pl. 3, fig. 1; Frederiksen, 1980b, p. 150, pl. 1, fig. 2; Jaramillo and Dilcher, 2001, p. 98, pl. 1, fig. 11-13; Harrington, 2003b, pl. 1, fig. 19; Jardine and Harrington, 2008, pl. 1, fig. 5.

Cicatricosisporites paradorogensis Krutzsch, 1959a, p. 172, pl. 35, fig. 366-371; pl. 36, fig. 372-373; Frederiksen, 1980a, p. 32, pl. 3, fig. 4; Jardine and Harrington, 2008, pl. 1, fig. 6.

Dimensions. Equatorial diameter 31 – 56 μm , mean 46 μm (four specimens measured); polar diameter 43 μm (one specimen measured). Potonié and Gelletich (1933) gave a range of 59 – 68 μm for the protologue specimens. Srivastava (1972) gave a range of 30-59 μm for specimens from the Naheola Formation of Alabama.

Remarks. The major distinguishing features of this form-species have been detailed in the genus remarks. The striae of *Cicatricosisporites dorogensis*, as illustrated by Potonié and Gelletich (1933), are continuous to partially foveolate (Srivastava, 1972).

Cicatricosisporites dorogensis therefore overlaps morphologically with *Cicatricosisporites paradorogensis* Krutzsch 1959, which has distinctly foveolate striae. Furthermore, Frederiksen (1980b) noted that many specimens of *Cicatricosisporites* from the Gulf and Atlantic Coastal Plains are intermediate between *Cicatricosisporites dorogensis* and *Cicatricosisporites paradorogensis*. The two forms also appear to have little stratigraphic utility. Most of my specimens have more or less continuous striae and therefore better correspond with *Cicatricosisporites dorogensis*, although intermediate to distinctly foveolate forms (e.g. the specimen illustrated as *Cicatricosisporites paradorogensis* in Jardine and Harrington (2008)) were observed also. It is therefore hard to differentiate these forms consistently, and I have followed Frederiksen (1980b) and assigned all striate trilete spores in my samples to *Cicatricosisporites dorogensis*.

Elsik (1968a) recorded forms intermediate between *Cicatricosisporites dorogensis* and *Microreticulatisporites*, which may correspond to *Cicatricosisporites paradorogensis*. As such, I have included these in *Cicatricosisporites dorogensis* in this study.

Botanical affinity. Schizaeaceae (Srivastava 1972). Frederiksen (1980a) suggested an affinity with the schizaceous genera *Anemia* or *Mohria*.

Occurrence. Occurred in relative abundances of <12% in 115/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon is known to range up into the Early Oligocene Vicksburg Formation on the eastern Gulf Coast (Frederiksen, 1980a), and is generally common in the upper Mesozoic and Cenozoic (Srivastava, 1972).

Genus *Cingulatisporites* Thomson in Thomson & Pflug 1953 emend. Hiltman 1967

Type species. *Cingulatisporites levispeciosus* Pflug in Thomson & Pflug 1953

Remarks. These trilete spores are distinguished from other spore genera by the

presence of a cingulum, which does not exceed 1/3 of the spore radius in width. The exine is psilate to finely scabrate, and the trilete mark is long, thin and simple. Spores of *Stereisporites* that do not possess an exine sculpture, such as *Stereisporites stereoides*, are similar to smaller forms of *Cingulatisporites*, with the exception of the cingulum in the latter genus.

Cingulatisporites spp.

Plate 2, figure 1

Cingulatisporites sp. Jardine and Harrington, 2008, pl. 1, fig. 12.

Dimensions. Equatorial diameter 24 – 26 µm (two specimens measured).

Remarks. I have assigned to *Cingulatisporites* spp. spores that are small, trilete and possess a cingulum. The amb is sub-triangular with convex sides to almost circular, and the exine is smooth. Sphagnaceous spores illustrated by Elsik (1968a) as *Sphagnum stereoides* (Potonié & Venitz 1934) Martin & Rouse 1966 and *Sphagnum bujargiensis* (Bolthovitina 1956) Elsik 1968 possess a cingulum, and may represent *Cingulatisporites*. Given the rarity and lack of stratigraphic utility of *Cingulatisporites* spp., I have not attempted to subdivide to species level.

Botanical affinity. *Sphagnum* Linnaeus (Sphagnaceae) (Elsik, 1968a; Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <2% in 50/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Deltoidospora* Miner 1935

Type species. *Deltoidospora hallii* Miner 1935.

Remarks. This genus represents generalised trilete spores with concave-triangular to almost circular amb. The exine is psilate to infrapunctate, and the laesurae is distinct, extends at least 2/3 from the pole to the equator, and may be bordered by folds. *Cyathidites* Couper 1953 has distinctly concave sides, *Toroisporites* has distinct tori bordering the laesurae, *Granulatisporites* has a granulate exine, and *Leiotriletes* and *Punctatisporites* are distinctly punctate.

Deltoidospora spp.

Plate 1, figure 15

cf. *Cyathidites minor* Couper 1953. Elsik, 1968a, p. 292, 294, pl. 8, fig. 2.

Deltoidospora sp. Elsik, 1968a, p. 294, pl. 8, fig. 3; Harrington, 2003b, pl. 1, fig. 34;

Jardine and Harrington, 2008, pl. 1, fig. 9.

Lygodiumsporites adriennis (Potonié & Gelletich 1933) Potonié 1956. Frederiksen, 1980a, p. 30, pl. 1, fig. 12-13.

Lygodiumsporites? cf. *L. adriennis* (Potonié & Gelletich 1933) Potonié 1956. Frederiksen, 1980a, p. 30, pl. 1, fig. 12-13.

Dimensions. Equatorial diameter 29 – 66 μm , mean 48 μm (nine specimens measured); polar diameter 44 – 70 μm , mean 54 μm (six specimens measured).

Remarks. I have assigned to *Deltoidospora* spp. large, trilete spores with thick, psilate to infra-punctate exine, and concave-triangular to subcircular amb. I have not attempted to assign *Deltoidospora* types to form species level because of the difficulty of doing so consistently, and the lack of stratigraphic value in doing so. I have also not attempted to distinguish between *Deltoidospora* and *Cyathidites* Couper 1953,

because of the difficulties of separating consistently between these similar form genera, especially when morphological changes due to transport, taphonomy and sample processing are taken into account. Some of these specimens have slight folds bordering the laesurae, especially when the laesurae are gaping open. However, I have assigned deltoid spores with distinct tori to *Toroisporites*.

Botanical affinity. Probably Cyatheaceae or Schizaceae. Some specimens may represent *Lygodium* Swartz (Lygodiaceae) (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <36% in 147/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Gleicheniidites* Ross 1949 emend. Skarby 1964

Type species. *Gleicheniidites senonicus* Ross 1949 emend. Skarby 1964.

Remarks. *Gleicheniidites* describes trilete spores with inter-radial crassitudes. The amb is triangular with rounded apices, and the exine is psilate or indistinctly sculptured. *Camarazonosporites* (Pant 1954 ex Potonié 1956) Klaus 1960 also has inter-radial crassitudes but has a well-rounded amb and a distal rugulate sculpture. *Toroisporis* Krutzsch 1959 has thickenings bordering the laesurae, rather than in the inter-radial areas.

Gleicheniidites senonicus Ross 1949 emend. Skarby 1964

Plate 2, figure 2

Gleicheniidites senonicus Ross, 1949, p. 31, pl. 1, fig. 3.

Gleicheniidites senonicus Ross, emend. Skarby, 1964, p. 65-67, text-fig. 1, pl. 1-3;

Frederiksen, 1980a, p. 29-30, pl. 1, fig. 8.

Gleicheniidites sp. Elsik, 1968a, pl. 8, figs. 8-9.

Gleicheniidites spp. Pocknall and Nichols, 1996, p. 9, pl. 1, fig. 6.

Dimensions. Equatorial diameter 23 – 26 μm , mean 25 μm (three specimens measured). Skarby (1964) gave measurements of about 30 μm .

Remarks. The major morphological attributes of this species have been detailed in the genus remarks. In my material the majority of these spores had concave-triangular amb. with well-rounded corners. Inter-radial crassitudes are always present, and the laesurae are long and thin and reach the equator.

Botanical affinity. Gleicheniaceae (Frederiksen, 1980a; Pocknall and Nichols, 1996). Skarby (1964) suggested *Gleichenia* or *Dicranopteris* as suitable extant genera.

Occurrence. Occurred in relative abundances of <1% in 13/151 samples, from the Porters Creek to the Hatchetigbee formations. On the Gulf Coast this taxon ranges up to the Early Oligocene Vicksburg Group (Frederiksen, 1980a). Similar forms have also been recorded from the Paleocene of the Western Interior (Pocknall and Nichols, 1996).

Genus *Granulatisporites* Ibrahim 1933 emend. Potonié & Kremp 1954

Type species. *Granulatisporites granulatus* Ibrahim 1933.

Remarks. This genus includes granulate trilete spores with a triangular to rounded triangular amb. The granula are evenly distributed over the spore surface, and are circular in plan view and rounded or flat in section. This genus differs from other more or less triangular trilete spores in lacking thickenings around the trilete mark (e.g. *Toroisporites*) or the equator (e.g. *Cingulatisporites*, *Camarazonosporites*), and having a granulate exine sculpture.

Granulatisporites luteticus (Krutzsch 1959) Frederiksen 1980

Plate 2, figure 3

Punctatisporites luteticus Krutzsch, 1959a, p. 68, pl. 4, figs. 25-26.

Granulatisporites luteticus (Krutzsch) Frederiksen, 1980a, p. 31, pl. 2, fig. 13.

Granulatisporites sp. Harrington, 2003b, pl. 1, figs. 33, 35-36.

Dimensions. Equatorial diameter 28 – 41 μm , mean 36 μm (four specimens measured). Krutzsch (1959a) gave a range of 50 – 70 μm for the protologue specimens.

Remarks. *Granulatisporites luteticus* includes trilete spores with a granulate exine. The amb is triangular with rounded apices, and the sides are straight to slightly concave or convex. The rays of the trilete mark are straight and extend 1/2 to 3/4 the radius of the grain.

Botanical affinity. Frederiksen (1980a) likened this morphospecies to spores of *Acrostickum aureum* Linnaeus (Pteridaceae).

Occurrence. Occurred in relative abundances of <6% in 25/151 samples, from the base of the Hatchetigbee Formation to the top of the Tallahatta Formation. This species is known to range into the Late Eocene Yazoo Clay on the eastern Gulf Coast (Frederiksen, 1980a).

Genus *Leiotriletes* Naumova 1939 ex. Ishchenko 1952 emend. Potonié & Kremp 1954

Type species. *Leiotriletes sphaerotriangulus* (Loose in Potonié, Ibrahim and Loose 1932) Potonié & Kremp 1954.

Remarks. As emended by Potonié and Kremp (1954), *Leiotriletes* describes infrapunctate trilete spores with strongly triangular amb. It can therefore be

distinguished from *Punctatisporites* Ibrahim 1933, which includes infrapunctate trilete spores with circular ambis.

Leiotriletes spp.

Plate 2, figure 4

Dimensions. Equatorial diameter 22 – 28 μm , mean 26 μm (three specimens measured).

Remarks. These spores are small, have triangular ambis with straight to concave sides, and are infrapunctate. The laesurae is thin and typically reaches 2/3 to 3/4 of the way to the equator. Preservation was often poor; many specimens appeared folded or split. It was therefore difficult to consistently recognise distinct morphological groups within this form genus, and since it has little stratigraphic value, no attempt was made to identify specimens to species level.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <3.2% in 95/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Microreticulatisporites* Knox 1950 emend. Potonié & Kremp 1954

Type species. *Microreticulatisporites lacunosus* (Ibrahim 1933) Knox 1950.

Remarks. *Microreticulatisporites* includes reticulate trilete spores. The lumina are under 6 μm wide and may be irregular in shape, this latter feature being caused by branching muri. The amb is triangular to circular, and the spore outline is crenulate to undulate. *Retitriletes* and *Zlivisporis* have reticula that are mostly limited to the distal face of the grain.

Microreticulatisporites spp.

Plate 2, figure 6

Microreticulatisporites spp. Elsik, 1968a, p. 306, pl. 12, figs. 1-8.

Dimensions. Equatorial diameter 26 – 41 μm , polar diameter 38 – 39 μm (two specimens measured).

Remarks. This taxon describes reticulate, trilete, triplanoid spores. My specimens of *Microreticulatisporites* spp. match closely with those illustrated by Elsik (1968a). The muri are 2.5 – 4 μm thick, discontinuous, and have smooth, rounded crests; the lumina are rounded in shape and at least twice as wide as the muri. This taxon appears to intergrade morphologically with *Cicatricosisporites dorogensis* (e.g. Elsik, 1968a; pl. 13, fig. 6.), with intermediate forms being described by *Cicatricosisporites paradorogensis* Krutzsch 1959. In my material those forms that are predominantly striate were recorded as *Cicatricosisporites dorogensis*, and those that were predominantly reticulate were recorded as *Microreticulatisporites* spp.

Affinity. Unknown.

Occurrence. Occurred in 39/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. In most samples relative abundances were <3%; however in the lowermost lignite sample from the Red Hills Mine (uppermost Nanafalia Formation) *Microreticulatisporites* spp. comprised 11.5% of the pollen count.

Genus *Patellasporites* Groot & Groot 1962

Type species. *Patellasporites tavaresensis* Groot & Groot 1962

Remarks. This genus includes spores with a convex-triangular to circular amb, and

a patella (an outer structure that encloses the distal and equatorial surfaces). The proximal face is typically smooth, and the patella may be smooth or ornamented, and is often dissected by narrow canals. The Palaeozoic genus *Murospora* Somers 1952 is concave-triangular and may be patellate or fully capsulate (i.e. the outer structure completely encloses the spore).

Patellasperites spp.

Plate 2, figure 5

Dimensions. Equatorial diameter 28 – 71 μm , mean 52 μm (five specimens measured).

Remarks. The spores assigned to this taxon were variable in size and morphology, but all conformed to the genus diagnosis for *Patellasperites*. The grains were frequently corroded or showed fungal scars, and the patellae were rarely entire around the equator of the grain. Canals on the distal surface of the grain were not observed. Given the rarity and morphological variability of these forms, I have not tried to subdivide them to below genus-level.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 5/151 samples, in the Porters Creek and Naheola formations on the eastern Gulf Coast.

Genus *Punctatisporites* Ibrahim 1933 emend. Potonié & Kremp 1954

Type species. *Punctatisporites punctatus* (Ibrahim in Potonié, Ibrahim and Loose 1932) Ibrahim 1933.

Remarks. This genus includes trilete spores with an infrapunctate exine, and a circular amb. It therefore differs from *Leiotriletes*, which has an infrapunctate exine

and a triangular amb.

Punctatisporites spp.

Plate 2, figure 7

Dimensions. Equatorial diameter 33 – 40 μm , mean 37 μm (three specimens measured).

Remarks. I have included all infrapunctate, trilete spores with circular amb. in *Punctatisporites* spp. All spore outlines were smooth and therefore the exine sculpture was infrapunctate rather than punctate. Given the rarity of these forms and their lack of stratigraphic value, I did not attempt to separate them into form-species.

Affinity. Unknown.

Occurrence. Occurred in relative abundances of <1.1% in 13/151 samples, from the Tusahoma to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Retitriletes* Pierce emend. Doring et al. in Krutzsch 1963

Type species. *Retitriletes globosus* Pierce 1961.

Remarks. This form genus includes trilete spores with a reticulate exine on the distal face. The proximal face is often psilate but the reticulum may extend over the equator to the trilete mark. The genus *Lycopodiumsporites* Thiergart ex Delcourt and Sprumont 1955 is foveo-reticulate on the distal face only, and *Klukisporites* Couper 1958 is foveolate to foveo-reticulate on both faces (Srivastava, 1972). *Microreticulatisporites* is reticulate on both faces of the grain, and has relatively thick muri that may branch, and thus influence the shape of the lumina.

Retitriletes spp.

Plate 2, figures 8-10

Dimensions. Equatorial diameter 26 – 55 μm , mean 34 μm (12 specimens measured).

Remarks. This taxon represents reticulate trilete spores with rounded triangular to subcircular outlines. The reticulum on all specimens is in the form of a widely spread but thin mesh. The lumina are typically pentagonal or hexagonal, and relatively homobrochate across the spore surface. Lumina diameters range from 3 – 6 μm among the specimens in this taxon. The muri are uniformly $<0.5 \mu\text{m}$ wide and 1 – 4 μm high. The trilete mark ranges from distinct to indistinct, but is always long and typically reaches the equator.

Affinity. Lycopodiaceae (Srivastava, 1972).

Occurrence. Occurred in relative abundances of $<3.1\%$ in 52/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Stereisporites* Pflug in Thomson & Pflug 1953

Type species. *Stereisporites stereoides* (Potoné & Venitz 1934) Pflug in Thomson & Pflug 1953.

Remarks. This form genus describes small, trilete spores of sphagnaceous affinity. The amb is convex triangular with rounded apices, and the trilete mark is simple, straight and lacks tori. The exine is two layered. Spores of *Stereisporites* are similar to those of *Cingulatisporites* (Thomson in Thomson & Pflug 1953) Hiltman 1967, but differ in that the former lack a well-developed cingulum.

Stereisporites granistereooides Krutzsch 1963

Plate 2, figure 11

Stereisporites granistereooides Krutzsch et al., 1963, p. 82, pl. 22, figs. 5 – 13a.

Sphagnum bimammatus (Naumova ex Bolkhovitina 1953) Elsik, 1968a, p. 304, 306, pl. 11, figs. 1-2.

Dimensions. Equatorial diameter 25 – 28 μm , mean 26 μm (four specimens measured). Krutzsch et al. (1963) gave an equatorial diameter of 25 – 28 μm for the protologue specimens.

Remarks. This taxon accommodates sphagnaceous spores with a distal verrucate sculpture. The amb is undulating and the corners are often thickened. *Stereisporites granulus* Krutzsch 1963 is smaller and has a thinner wall and a finer sculpture. Specimens recorded as *Stereisporites* sp. cf. *S. granistereooides* by Pocknall and Nichols (1996) are similar but smaller, with an equatorial diameter of 18 – 22 μm .

Botanical affinity. *Sphagnum* (Sphagnaceae).

Occurrence. Occurred in relative abundances of <1.6% in 15/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Stereisporites stereooides (Potonié & Venitz 1934) Pflug in Thomson & Pflug 1953

Plate 2, figure 12

Sporites stereooides Potonié and Venitz, 1934, p. 11-12, pl. 1, figs. 4-5.

Stereisporites stereooides (Potonié & Venitz) Thomson and Pflug, 1953, p. 53, pl. 1, figs. 64-73; Jardine and Harrington, 2008, pl. 1, fig. 11.

Sphagnum stereooides (Potonié & Venitz) Martin and Rouse, 1966, p. 184, pl. 1, figs. 3; Elsik, 1968a, p. 299, pl. 10, fig. 8; Frederiksen, 1980a, p. 34, pl. 4, figs. 13.

Dimensions. Equatorial diameter 28 μm (one specimen measured). Potonié and Venitz (1934) gave an equatorial diameter of 24 – 25 μm .

Remarks. I have used *Stereisporites stereoides* to describe small, rounded triangular trilete spores with relatively thick, unsculptured exines and long, simple laesurae. I have assigned similar forms possessing a distal verrucate exine to *Stereisporites granistereoides*.

Botanical affinity. *Sphagnum* (Sphagnaceae).

Occurrence. Occurred in relative abundances of <3% in 83/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. On the Gulf Coast this taxon is known to range into the Early Eocene Vicksburg Group. It is common globally from the Cretaceous onwards.

Genus *Toroisporis* Krutzsch 1959

Type species. *Toroisporites torus* (Pflug in Thomson & Pflug 1953) Krutzsch 1959

Remarks. This genus describes trilete spores with thickenings (tori) bordering the laesurae. The exine is smooth and the amb is rounded triangular to subcircular. There are no equatorial thickenings. *Deltoideospora* lacks tori but is otherwise similar. *Gleicheniidites* has inter-radial thickenings, rather than tori.

Toroisporis spp.

Plate 2, figure 13

Dimensions. Equatorial diameter 30 – 35 μm , mean 33 μm (three specimens measured).

Remarks. The position, size and shape of the tori in *Toroisporis* spp. are variable

among specimens. This taxon therefore represents a heterogeneous group of torate trilete spores. It was difficult to consistently assign these forms to distinct morphological groups, and there appears to be little advantage in doing so. I therefore did not separate below form-genus level.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 14/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Zlivisporis* Pacltová 1961

Type species. *Zlivisporis blanensis* Pacltová 1961.

Remarks. *Zlivisporis* includes trilete spores with a sparse, net-like reticulum on the distal face. The lumina are large and predominantly hexagonal in shape; the muri are very thin. The proximal face is psilate and the amb is subcircular. *Retitriletes* possesses a reticulum with wider and higher muri and smaller lumina, which may extend over onto the proximal face of the grain. *Microreticulatisporites* is reticulate on both the proximal and distal faces, and has lumina less than 6 µm wide.

Zlivisporis novamexicanum (Anderson 1960) Leffingwell 1971

Plate 2, figure 18

Lycopodium novamexicanum Anderson, 1960, p. 14, pl. 1, fig. 2; pl. 8, fig. 1.

Zlivisporis novamexicanum (Anderson) Leffingwell, 1971, p. 25, pl. 4, figs. 3-4; Jardine and Harrington, 2008, pl. 1, fig. 10.

Dimensions. Equatorial diameter 39 – 50 µm, mean 44 µm (four specimens)

measured). Anderson (1960) gave a range of 42 – 60 μm for the protologue specimens.

Remarks. In this species the amb is circular to subcircular and the laesurae are indistinct and reach the equator. The muri are $\sim 0.5\ \mu\text{m}$ wide and the lumina are 8 – 10 μm wide. *Lycopodium perplicatum* Bolkhovitina 1956 has a more distinct trilete mark, and *Zlivisporis blanensis* possesses larger lumina and muri.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of $<1.5\%$ in 26/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

BISACCATE POLLEN

Plate 2, figure 19; plate 3, figures 1-4

Dimensions. Grain length 51 – 75 μm , mean 64 μm (five specimens measured); height in equatorial view 41 μm (one specimen measured); width in polar view 41 – 60 μm , mean 50 μm (four specimens measured).

Remarks. Bisaccate pollen previously reported from the GCP has been assigned to the extant genera *Pinus* Linnaeus, *Picea* Dietrich, *Cedrus* Trew (all Pinaceae), or *Podocarpus* Persoon (Podocarpaceae); or to the form-genus *Pityosporites* Seward 1914 emend. Manum 1960 (Elsik, 1968a; Frederiksen, 1980a). These genera are distinguished from each other via corpus and sacchi dimensions, mode of sacchi attachment, and exine structure and ornamentation. The specimens in my samples were often poorly preserved, or orientated so that diagnostic features were obscured. Consistent genus-level assignments were therefore not possible, and for the purposes of making counts I have followed Pocknall and Nichols (1996) in combining all bisaccate pollen into one taxon. Given the high transport potential of bisaccate

grains (Faegri and van der Pijl, 1971; Nichols, 1995; van der Kaars, 2001), many of these specimens potentially had an extra-regional origin, limited the ecological interpretability of genus-level taxonomic assignments. These taxa also appear to be of limited use biostratigraphically.

Botanical affinity. Most of my bisaccate specimens can probably be assigned to the Pinaceae, but whether they could be linked confidently to any extant genus is questionable.

Occurrence. Occurred in relative abundances of <39% in 137/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

INAPERTURATE POLLEN

Genus *Cupressacites* Bolkhovitina 1956 ex. Krutzsch 1971

Type species. *Cupressacites russeus* Bolkhovitina 1956 ex. Krutzsch 1971.

Remarks. This genus comprises rounded, inaperturate pollen without a ligula. The exine is smooth to chagrinate and thin, and the grain often appears folded or split open. This genus differs from *Sequoiapollenites* in not possessing a ligula, and by frequently being split open.

Cupressacites hiatipites (Wodehouse 1933) Krutzsch 1971

Plate 3, figure 5

Taxodium hiatipites Wodehouse, 1933, p. 493, fig. 17; Wilson and Webster, 1946, p. 275, fig. 6; Rouse, 1962, p. 210, pl. 2, fig. 4; Elsik, 1968a, p. 307-308, 310, pl. 14, figs. 2a-b. *Cupressacites hiatipites* (Wodehouse) Krutzsch, 1971, p. 41; Frederiksen, 1980a, p. 36, pl. 6, fig. 6; Harrington, 2003b, pl. 1, fig. 15; Jardine and Harrington, 2008, pl. 1, fig.

15.

Taxodiaceapollenites hiatipites (Wodehouse) Frederiksen, 1980b, p. 151, pl. 1, figs. 4-5;
Frederiksen et al., 1983, p. 29, pl. 7, figs. 4-5.

Inaperturate pollen Pocknall and Nichols, 1996 [in part], p. 11-12, pl. 1, figs. 19-21.

Dimensions. Grain diameter 23 – 33 μm , mean 27 μm (eight specimens measured).
Wodehouse (1933) gave a range of 29 – 37 μm for the protologue specimens.

Remarks. I have differentiated inaperturate conifer pollen into two morphological groups: *Cupressacites hiatipites* represents grains with thin exine that are frequently split open, and *Sequoiapollenites* spp. represents grains that have a thicker exine and possess a ligula. *Cupressacites hiatipites* types were the most commonly observed of the two forms.

Cupressacites hiatipites grains have smooth to chagrinata to weakly granulate exines. They were probably initially spheroidal (Pocknall and Nichols, 1996), but the vast majority (>90%) of specimens were split open, and unsplit specimens were folded. The presence of split and unsplit specimens may reflect the differential preservational potential of different cupressaceous taxa (Pocknall and Nichols, 1996), but it could be a result of chance degradation during transport, sedimentation or preparation. I have therefore counted them together.

Botanical affinity. Cupressaceae; possibly *Taxodium* or *Glyptostrobus* (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <53% in 150/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. On the Gulf Coast this taxon is known to range into at least the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Genus *Ephedripites* Bolkovitina 1953 ex. Potonié 1958

Type species. *Ephedripites mediolobatus* Bolkovitina 1953 ex. Potonié 1958.

Remarks. This form genus contains pollen comparable to the extant genus *Ephedra* Linnaeus. The grains are elliptical in equatorial view, and have an outer exinal layer that forms longitudinal ribs. These may run \pm parallel to the polar axis, or at an angle to it.

Ephedripites subgenus *Spiralipites* spp.

Plate 3, figure 6

Ephedra voluta Stanley, 1965, p. 284-285, pl. 40, figs. 10-11; Elsik, 1968a, p. 307, pl. 14, fig. 3-7.

Ephedra? aff. *E. voluta* Frederiksen, 1979, p. 162, pl. 4, fig. 38.

Ephedra? *laevigataeformis* (Bolkhovitina 1961) Frederiksen, 1980a, p. 37, pl. 7, fig. 5.

Ephedripites sp.2 Frederiksen et al., 1983, p. 31, pl. 7, fig. 21.

Ephedripites subgenus *Spiralipites* spp. Frederiksen, 1988, pl. 1, fig. 5.

Dimensions. Length 48 – 50 μm , width 26 – 29 μm (two specimens measured). Elsik (1968a) recorded similar specimens measuring 35 – 45 μm by 15 – 23 μm from the Late Paleocene of Texas, and Frederiksen et al. (1983) recorded one specimen with a length of 35 μm from the Middle Eocene of California.

Remarks. This subgenus of *Ephedripites* has ribs that run at an angle to the polar axis, and wrap around the grain. There are no zig-zag lines on the grain surface between the ribs (Kruttsch, 1970). Although *Spiralipites* types are structurally similar to extant *Ephedra* pollen (Frederiksen et al., 1983) and pollen assigned to the extant genus has previously been reported from the US Gulf Coast (e.g. *Ephedra exigua* Frederiksen 1980 and *Ephedra hungarica* [Nagy 1963] Frederiksen 1980), there is uncertainty with

assigning pollen of this subgenus to *Ephedra*, as demonstrated by Frederiksen's (1979, 1980a) use of *Ephedra*? for similar forms. I have therefore not attempted to use the extant genus, and given the rarity and morphological similarity of these pollen types I have not assigned them to below subgenus level.

Botanical affinity. Possibly *Ephedra* (Ephedraceae).

Occurrence. Occurred in relative abundances of <1% in 6/151 samples, in the Porters Creek and Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This subgenus is known to range from the Cretaceous (Fairchild and Elsik, 1969) to the Middle Eocene (Frederiksen, 1980a) on the US Gulf Coast, although some of these younger occurrences may be reworked from older strata (Frederiksen, 1980a, b).

Genus *Sequoiapollenites* Potonié 1958

Type species. *Sequoiapollenites poliformosus* (Thiergart 1938) Potonié 1958

Remarks. This form genus includes ligulate, inaperturate pollen. The grains are more or less spherical, and have a smooth to weakly granulate exine. Aside from the diagnostic presence of a ligula, these grains can be further differentiated from other inaperturate conifer pollen by the thicker exine resulting in a more stable (i.e. less folded) grain form.

Sequoiapollenites spp.

Plate 3, figure 7

Inaperturate pollen, Pocknall and Nichols, 1996 [in part], p. 11-12, pl. 1, fig. 17-18?

Sequoiapollenites sp. Jardine and Harrington, 2008, pl. 1, fig. 16.

Dimensions. Equatorial diameter 24 μm (two specimens measured).

Remarks. This taxon includes inaperturate pollen possessing a ligula. This form has a more rigid exine than *Cupressacites hiatipites*, and therefore did not appear folded or split in my samples. The exine is finely granulate, and the ligula are 2-3 μm long.

Botanical affinity. Cupressaceae. This taxon may represent *Sequoia*.

Occurrence. Occurred in relative abundances of <5% in 61/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

MONOPORATE POLLEN

Genus *Milfordia* Erdtman 1960 emend. Krutzsch 1970

Type species. *Milfordia hypolaenoides* Erdtman 1960

Remarks. This form genus describes monoporate (not monocolpate, as Erdtman (1960) initially stated) pollen with a punctate to foveolate exine. The amb is spherical to lenticular. *Milfordia* can be distinguished from *Sparganiaceapollenites* by its punctate to foveolate, rather than reticulate, exine. *Graminidites* Cookson 1947 ex Potonié 1960 differs in being granulate.

Milfordia hungarica (Kedves 1965) Krutzsch & Vanhoorne in Krutzsch 1970

Plate 3, figures 8-9

Monoporopollenites hungaricus Kedves, 1965, p. 50-51, Text-Figures 1-6.

Monulcipollenites confossus Fairchild in Stover et al., 1966, p. 3, pl. 1, figs. 5a, b.

Milfordia hungarica (Kedves) Krutzsch and Vanhoorne in Krutzsch 1970, p. 74, 76, pl. 10, figs. 1-3; Frederiksen in Frederiksen et al., 1983, p.32, pl. 8, figs. 1-2.

Dimensions. Equatorial diameter 31 – 43 μm , mean 37 μm (10 specimens measured). Fairchild in (in Stover et al., 1966) recorded grain diameters of 30 to 44 μm for the junior synonym *Monulcipollenites confossus* in the Early Eocene of Texas. Frederiksen (in Frederiksen et al., 1983) recorded diameters of 42-59 μm from specimens from the Middle Eocene of California.

Remarks. Two species of *Milfordia* pollen were recovered from my samples, which are similar in all respects other than size: *Milfordia hungarica* is over 30 μm in equatorial diameter, and *Milfordia minima* is under 30 μm . Both are foveolate, monoporate with a small pore and weak annulus, and have a circular amb. The two taxa have different stratigraphic ranges (Frederiksen in Frederiksen et al., 1983), justifying their taxonomic differentiation based purely on size. This taxon has a maximum diameter of about 60 μm (Frederiksen, 1979), but I observed no specimens over 43 μm .

Botanical affinity. Restionaceae or *Joinvillea* (Joinvilliaceae) (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <7% in 8/151 samples, from the Hatchetigbee to the Tallahatta formations on the eastern Gulf Coast. This taxon has not been recorded above the Middle Eocene on the Gulf Coast (Frederiksen, 1988).

Milfordia minima Krutzsch 1970

Plate 3, figure 10

Restioniidites hungaricus (Kedves 1965) Elsik, 1968a, p. 313, pl. 15, fig. 13.

Milfordia minima Krutzsch, 1970, p. 76, pl. 10, figs. 4-34; Frederiksen, 1979, p. 139-140, pl. 1, fig. 14; Frederiksen, 1980a, p. 38, pl. 7, fig. 8; Frederiksen, 1980b, pl. 1, fig. 12-13.

Dimensions. Equatorial diameter 26 – 29 μm , mean 28 μm (three specimens measured).

Remarks. *Milfordia minima* is similar to *Milfordia hungarica*, apart from the former species' smaller size.

Botanical affinity. Restionaceae or *Joinvillea* (Joinvilliaceae) (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <5% in 11/151 samples, from the Hatchetigbee to the Tallahatta formations on the eastern Gulf Coast. In my samples *M. minima* was more common in the Hatchetigbee Formation, and *M. hungarica* was more common in the Tallahatta Formation. In the southeastern United States (eastern Gulf Coast and South Carolina) *M. minima* is known to range from the Early Paleocene to the Early Oligocene (Frederiksen, 1979).

Genus *Sparganiaceapollenites* Thiergart 1937

Type species. *Sparganiaceapollenites polygonalis* Thiergart 1937

Remarks. This genus describes ± spherical, monoporate pollen with a reticulate exine. The pore is small and round and without an annulus. The exine is columellate and semi-ectate. *Milfordia* differs in being punctate to foveolate rather than reticulate. *Retiovoipollis* Krutzsch 1970 differs in being distinctly oval.

Sparganiaceapollenites spp.

Plate 3, figure 11

Sparganiaceapollenites sp. Jardine and Harrington, 2008, pl. 2, fig. 1.

Dimensions. Equatorial diameter 28 µm (one specimen measured).

Remarks. Previously illustrated specimens of *Sparganiaceapollenites* from the Gulf Coast (Frederiksen, 1988), South Carolina (Frederiksen, 1980b), Virginia (Frederiksen,

1979) and the Western Interior (Pocknall and Nichols, 1996), have varied in terms of pore size, presence of an annulus, grain size and style of reticulation. My specimens exhibit much of this previously documented variation. Lumina width was mostly ~ 1 µm, which is most similar to *Sparganiaceapollenites* sp. of Frederiksen (1980b) and *Sparganiaceapollenites* cf. *S. reticulatus* of Frederiksen (1988). These morphotypes differ in the presence of an annulus, albeit indistinct, in the latter taxon. Unfavourable orientation of grains meant that pore details could not be ascertained in many of my specimens, making consistent species-level assignments difficult. I have therefore only classified these forms to genus level.

Botanical affinity. Probably Sparganiaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <6.5% in 60/151 samples, from the Naheola to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

TRIPORATE POLLEN

Genus *Basopollis* Pflug 1953

Type species. *Basopollis orthobasilis* (Pflug in Thomson & Pflug 1953) Pflug 1953

Remarks. *Basopollis* is a Normapolle genus incorporating triporate grains with a triangular to concave-triangular amb. The sexine is psilate to punctate, and is thicker than the nexine. The pores are slit-shaped, vestibulate and complex, comprising several layers. The exogerminals are polyannulate, formed by bacula of different lengths projecting radially from the inner layer of the sexine. This feature distinguishes *Basopollis* from the otherwise similar *Complexiopollis* and *Choanopollis*.

Basopollis obscurocostatus Tschudy 1975

Plate 3, figure 12

Extratropopollenites basalis Pflug & Thomson in Thomson & Pflug 1953. Elsik, 1968b, p. 650, pl. 37, fig. 1.

Basopollis basalis (Pflug & Thomson) Pflug 1953. Fairchild and Elsik, 1969, p. 85, pl. 38, fig. 154.

Basopollis obscurocostatus Tschudy, 1975, p. 8, pl. 1, fig. 1-12; Text-Figure 1;

Frederiksen, 1979, p. 156, pl. 3, fig. 17-18; Jardine and Harrington, 2008, pl. 2, fig. 2.

Dimensions. Equatorial diameter 25 μm (two specimens measured). Tschudy (1975) gave a range of 28 – 42 μm for the protologue specimens.

Remarks. *Basopollis obscurocostatus* has a concave-triangular amb, equatorial arci, and a scrabrate to microverrucate exine sculpture. It possesses the polyannulate exogerminal diagnostic of this genus. My measured specimens are slightly smaller than Tschudy's (1975), but are otherwise in good agreement with his description. The concave-triangular amb, thin walls and presence of arci distinguish *Basopollis obscurocostatus* from *Basopollis orthobasalis*. *Basopollis basalis* differs from *Basopollis obscurocostatus* in having a smooth sexine (Tschudy, 1975).

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <4% in 13/151 samples, from the Porters Creek to the Tusahoma formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. One specimen was also recovered from the Meridian Sand Member of the Tallahatta Formation; this was probably reworked, but as this species has previously been recorded from the Hatchetigbee Formation (Tschudy, 1975) this may be a genuine occurrence.

Betulaceae/Myricaceae type

Plate 3, figures 13-14

Betulaceae-Myricaceae-Casuarinaceae complex. Leffingwell, 1971, p. 40.

Betulaceae-Myricaceae types. Elsik, 1974, pl. 2, figs. 39-40; Jardine and Harrington, 2008, pl. 2, fig. 11.

Betulaceae-Myricaceae. Elsik and Dilcher, 1974, pl. 29, figs. 98-101.

Triporopollenites spp. Pocknall & Nichols, 1996, p. 32, pl. 7, fig. 10-12.

Myricaceae/Betulaceae. Harrington, 2003b, pl. 1, fig. 20.

Dimensions. Equatorial diameter 18 – 45 μm , mean 27 μm (20 specimens measured).

Remarks. This taxon includes the genera *Triatriopollenites* Pflug in Thomson & Pflug 1953 and *Triporopollenites* Pflug in Thomson & Pflug 1953. Both genera describe pollen with three equatorial annulate to tumescent pores, a convex-triangular to subcircular amb, and granulate exine. Vestibula are never present. The two genera are distinguished by the presence of an atrium in *Triatriopollenites*, but this feature can be hard to consistently recognise under light microscopy, and separating these genera is therefore problematic. Splitting these genera into form species is similarly challenging, based as it is on fine-scale details of aperture morphology and exine structure. I have therefore followed previous authors (see synonymy list, above) in assigning all such morphotypes to one generalised, composite taxon.

Casuarinidites Cookson and Pike 1954 has also previously been used to accommodate triporate pollen recovered from the US Gulf Coast (Srivastava, 1972; Frederiksen and Christopher, 1978; Frederiksen, 1980a). This genus differs from *Triatriopollenites* and *Triporopollenites* in having a sexine that is thicker than the nexine. However, Frederiksen (1988) argued that North American pollen previously assigned to *Casuarinidites* is better represented by *Triatriopollenites* and *Triporopollenites*, and I have placed specimens similar to those previously assigned to

Casuarinidites in the Betulaceae/Myricaceae type.

The Betulaceae/Myricaceae type can be distinguished from *Trivestibulopollenites* in not having vestibulate pores. *Momipites* typically has less strongly annulate or tumescent pores, is less densely granulate, and frequently displays polar exine modifications. *Caryapollenites* has some or all of its pores displaced away from the equator and onto one hemisphere.

Botanical affinity. Betulaceae or Myricaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <82% in 151/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This was the most abundant morphotype in the dataset.

Genus *Brosipollis* Krutzsch 1968

Type species. *Brosipollis salebrosus* (Pflug in Thomson & Pflug 1953) Krutzsch 1968

Remarks. *Brosipollis* describes pollen with three equatorially protruding pores. The pores may be vestibulate or atriate; and are surrounded by strong labra or annuli that cause them to protrude from the otherwise circular amb. The exine surface may be psilate, punctate or striate. *Trivestibulopollenites* Pflug in Thomson and Pflug 1953 is vestibulate and has slightly protruding germinals, but labra or annuli are not strongly developed in this genus. *Myriophyllum* and its associated form genus *Haloragacidites* Couper 1958 have distinctly annulate pores that are not vestibulate or atriate. Tetraporate forms are also accommodated within these genera.

Brosipollis striata type

Plate 3, figures 15-16

Brosipollis striata Frederiksen, 1988, p. 52, pl. 3, fig. 23-26; pl. 4, fig. 1-3.

Brosipollis, other striate species. Frederiksen, 1988, pl. 4, fig. 5-6, 10-11.

Brosipollis sp. Harrington, 2003b, pl. 1, figs. 3-4.

Dimensions. Equatorial diameter 21 – 25 μm , mean 22 μm (seven specimens measured). Frederiksen (1988) gave a range of 21 – 26 μm for the protologue specimens.

Remarks. This taxon comprises pollen similar to *Brosipollis striata* Frederiksen 1988. Most specimens are triporate; one abnormal tetraporate grain was observed. All grains are finely striate; striae and lirae are $<0.5 \mu\text{m}$ wide, and run parallel to anastomosing. The pores are round and mostly lack vestibulae, although in some grains a weak vestibulum was present. My specimens fit well with Frederiksen's (1988) description in terms of size, but show variability in labra height. Some specimens have labra of 3-4 μm high (Plate 3, figure 16), and probably represent *B. striata sensu stricto*. Others have labra of just 1-2 μm high (Plate 3, figure 15), and match better with pollen grains illustrated by Frederiksen (1988) as *Brosipollis*, other striate species (e.g. Frederiksen, 1988, pl. 4, fig. 5-6, 10-11). As these different types were hard to consistently differentiate, I have included them in one morphotype. *Brosipollis striatobrosus* (Kruttsch 1961) Kruttsch 1968 is also striate, but is vestibulate and tricolporate.

Botanical affinity. Possibly *Bursera* (Burseraceae) (Frederiksen, 1988).

Occurrence. Occurred in relative abundances of $<2\%$ in 8/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast.

Genus *Caryapollenites* Raatz 1937 ex Potonié 1960 emend. Kruttsch 1961

Type species. *Caryapollenites simplex* (Potonié 1934) Raatz 1937.

Remarks. This genus includes pollen resembling that of modern *Carya* Nuttall (Juglandaceae). Grains are triporate with one or more pores being almost or

entirely subequatorial. The grains are oblate and the amb is rounded triangular to subcircular. The exine is finely granulate and typically thin; this latter feature often leading to secondary folding. The exine is often thinned, either as a circle, triangle or ring, at one pole. The pores are round and atriate, and only weakly labrate, if at all.

Subtriporopollenites Pflug & Thomson in Thomson & Pflug 1953 emend.

Krutzsch 1961 also has subequatorial pores but differs from *Caryapollenites* in lacking a polar thin area, and in having a more rigid exine that is distinctly columellate and (or) distinctly ornamented. *Momipites* demonstrates greater morphological variability in polar exine modifications, and pore position is limited to the equator of the grain. *Juglans* and *Juglanspollenites* Raatz 1937 accommodate pollen that typically has more than 3 pores (usually 6 – 18 pores in extant *Juglans* pollen) and may or may not be heteropolar (Nichols, 2010).

Caryapollenites imparalis group

Plate 3, figure 17

Caryapollenites imparalis Nichols and Ott, 1978, p. 105, pl. 2, fig. 4-6; Pocknall and Nichols, 1996, p. 26-27, pl. 6, fig. 16, Jardine and Harrington, 2008, pl. 2, fig. 3.

Caryapollenites inelegans Nichols and Ott, 1978, p. 105, pl. 2, fig. 7-8; Pocknall and Nichols, 1996, p. 27, pl. 6, fig. 17.

Dimensions. Equatorial diameter 26 – 29 μm , mean 28 μm (five specimens measured). Nichols and Ott (1978) gave a range of 29 – 35 μm for *Caryapollenites imparalis*, and 26 – 34 μm for *Caryapollenites inelegans*.

Remarks. *Caryapollenites imparalis* and *Caryapollenites inelegans* both contain *Carya*-like pollen without a developed polar thinning. Both have rounded triangular ambis with convex sides, and atriate pores. They differ in pore placement: in *Caryapollenites imparalis* two or more pores are partially subequatorial and form notches in the

amb outline, whereas in *Caryapollenites inelegans* all pores are entirely subequatorial and the amb is entire. This is a difficult diagnostic feature to apply in practice for two reasons. Firstly, these two morphotypes appear to be end members of a morphological continuum, and it is hard to assign specimens to one or the other consistently. Secondly, where grains are folded so that one or more pores are obscured, it can be difficult to determine the degree of pore displacement. I have therefore counted these two species together. Other species of *Caryapollenites* from the US Gulf Coast show exine thinning at one pole. *Carya viridifluminipites* (Wodehouse 1933) Wilson & Webster 1946, from the Western Interior of North America, is larger, at 35 – 40 μm (Nichols, 2010).

Botanical affinity. Juglandaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <7% in 109/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Caryapollenites veripites (Wilson & Webster 1946) Nichols & Ott 1978

Plate 3, figure 18

Carya veripites Wilson and Webster, 1946, p. 276, fig. 14.

Carya simplex (Potonié & Venitz 1934) Elsik, 1968b, p. 602, pl. 2, fig. 1; pl. 16, fig. 21-24.

Carya spp. <29 μm . Frederiksen and Christopher, 1978, p. 139, pl. 3, fig. 12 – 13;

Frederiksen, 1979, p. 150-151, pl. 2, fig. 17; Frederiksen, 1998, pl. 1, fig. 4.

Carya sp. 22 μ -28 μ . Tschudy, 1973a, p. B14, pl. 2, fig. 25-26.

Caryapollenites veripites (Wilson & Webster) Nichols and Ott, 1978, p. 106-107, pl. 2, fig. 12-13; Pocknall and Nichols, 1996, p. 27-28, pl. 6, fig. 18-19; Harrington, 2003b, pl. 1, fig. 21; Jardine and Harrington, 2008, pl. 2, fig. 4.

Carya sp. Frederiksen in Frederiksen et al., 1983, p. 35-36, pl. 9, fig. 20-21.

Dimensions. Equatorial diameter 24 – 31 μm , mean 28 μm (six specimens measured). Wilson and Webster (1946) gave a range of 27 – 33 μm for the protologue specimens; Nichols and Ott (1978) extended this range to 23 – 32 μm , with a modal diameter of 29 μm .

Remarks. *Caryapollenites veripites* has three atriate pores located entirely on one hemisphere, and a circumpolar ring of thinned exine surrounding a polar island of normal exine thickness. The exine is sparsely but evenly granulate, and the amb is rounded triangular with convex sides. Previous descriptions of *Carya*-like pollen from the US Gulf and Atlantic Coastal Plains (Tschudy, 1973a; Frederiksen and Christopher, 1978; Frederiksen, 1979) have recorded two populations of pollen similar to *Caryapollenites veripites* separated by size, with equatorial diameters above or below 29 μm . The smaller specimens occur in the Paleocene and range up into the Tallahatta Formation (Tschudy, 1973a), and larger specimens, which by their size resemble more closely modern *Carya* pollen, first occur in the Tallahatta Formation (Tschudy, 1973a) and range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a). *Caryapollenites veripites* is most similar to the smaller Gulf Coast *Carya* types in terms of size, but it does slightly overlap the 29 μm boundary. As all specimens observed in my samples fit within the size range given for *Caryapollenites veripites* by Nichols and Ott (1978), I have used this as a suitable form for species for my specimens, rather than using the informal size-based classification used by Tschudy (1973a) and Frederiksen (1978; 1979)

Caryapollenites veripites differs from the *Caryapollenites imparalis* Group by the presence of a circumpolar ring of thinned exine. It differs from *Caryapollenites wodehousei* by the fully subequatorial positioning of the pores in *Caryapollenites veripites* giving an entire, rather than notched, amb, and the constantly circular ring of thinned exine. In *Caryapollenites wodehousei* this ring varies in shape and is often triangular. *Caryapollenites veripites* differs from *Mompites* spp. that possess a circumpolar ring of thinned exine by the subequatorial position of its pores.

Botanical affinity. Juglandaceae, possibly *Carya* (Nichols and Ott, 1978).

Occurrence. Occurred in relative abundances of <6% in 77/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Caryapollenites wodehousei Nichols & Ott 1978

Plate 3, figure 19

Caryapollenites wodehousei Nichols and Ott, 1978, p. 106, pl. 2, fig. 9-11; Pocknall and Nichols, 1996, p. 28, pl. 6, fig. 20-21.

Carya? spp. Frederiksen and Christopher, 1978, p. 140, pl. 3, fig. 16 – 21, Frederiksen, 1979, 150-151.

Dimensions. Equatorial diameter 28 – 30 μm , mean 29 μm (four specimens measured). Nichols and Ott (1978) gave a range of 29-34 μm , with a modal diameter of 31 μm , for the protologue specimens.

Remarks. *Caryapollenites wodehousei* has a circular to triangular circumpolar ring of thinned exine, and two or more atriate pores displaced onto one hemisphere. The displacement is not complete, and the amb is notched. The amb is triangular in shape with convex sides and well-rounded corners. *Caryapollenites wodehousei* differs from *Caryapollenites veripites* in having a notched amb, and a circumpolar ring of thinned exine that is often triangular in shape. It differs from the *Caryapollenites imparalis* Group in having a circumpolar ring of thinned exine.

This taxon has previously been reported from the Gulf and Atlantic Coastal plains by Frederiksen and Christopher (1978) and Frederiksen (1979) as *Carya?* spp. Frederiksen and Christopher (1978) considered these forms to be transitional between true *Carya* pollen and their *Momipites tenuipolus* Group (occupied by *Momipites anellus* in the present study).

Botanical affinity. Juglandaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <3.4% in 31/151 samples, from the Nanafalia to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Choanopollenites* Stover in Stover et al. 1966

Type species. *Choanopollenites eximius* Stover in Stover et al. 1966.

Remarks. *Choanopollenites* is a Normapolle genus. The grains are triangular with straight to concave sides; often-bulging apical apertures enhance the concave nature of the grain sides. The grains are oblate and appear oval in equatorial view, although all grains recorded in my material were oriented in polar view. Exine sculpture is indistinct, with most species being smooth to scabrate. The sexine is distinctly thicker than the nexine. Stover (in Stover et al., 1966) stated that the pores in *Choanopollenites* are not vestibulate, but close examination of illustrations of the type species, *Choanopollenites eximius*, reveals that very thin vestibula are present in some specimens. Furthermore, in all of the species of *Choanopollenites* erected or transferred by Tschudy (1973b), vestibula of various sizes are present. A lack of vestibula is therefore not diagnostic for this genus. The exogerminals are in the form of lolongate slits in the sexine, and the endogerminals are lalongate and formed by nexinal flaps arranged perpendicular to the exogerminal. Individual species are distinguished based on grain size and shape, and the morphology of the apertures. *Choanopollenites* spp. were rare in my material, and with the exception of *Choanopollenites patricius* occurred as singletons in any one sample.

This genus shares with *Basopollis* and *Complexiopollis* a two-layered sexine around the exogerminals, with a structureless outer layer and an inner layer of radially projecting bacula. In *Choanopollenites* and *Complexiopollis* these bacula are of

an even length and so do not produce the polyannulate exogerminals characteristic of *Basopollis*. *Choanopollenites* is distinguished from *Complexiopollis* by lacking atriate germinals, possessing a thicker exine in which the sexine is thicker than the nexine, and being oval in equatorial view rather than triplane rhomboidal (Tschudy, 1973b).

Choanopollenites alabamicus (Srivastava 1972) Frederiksen 1979

Plate 3, figure 20

Extratropopollenites alabamicus Srivastava, 1972, p. 250, 252; pl. 12, fig. 1-11; pl. 13, fig. 11-3.

Choanopollenites transitus Tschudy, 1973b, p. C9, pl. 6, fig. 1-24; Text-Figure 8.

Choanopollenites alabamicus (Srivastava) Frederiksen, 1979, p. 155-156, pl. 3, fig. 12.

Dimensions. Equatorial diameter 22 – 25 μm (2 specimens measured). Srivastava (1972) gave a range of 18 – 26 μm for the protologue specimens. Tschudy (1973b) gave a range of 20 – 28 μm for his species *Choanopollenites transitus*, which is synonymous with *Choanopollenites alabamicus*.

Remarks. This taxon represents small grains of the basic *Choanopollenites*-type. The amb is concave-triangular and the baculate area around the germinal is large relative to the size of the grain. The surface of the grain is indistinctly scabrate. Srivastava (1972) emphasized the heteropolar nature of the grain in equatorial view, with one hemisphere being concave and the other convex. As all of my specimens were found in polar view, this feature was not observed. *C. alabamicus* is distinguished from *C. consanguineus* Tschudy 1973a by its strongly concave amb and prominent baculate areas. It can be distinguished from other species of *Choanopollenites* by its small size.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 4/151 samples, from the Porters Creek to the Nanafalia formations on the eastern Gulf Coast, and in the

Calvert Bluff Formation in Texas. This taxon ranges down into the Campanian on the US Gulf Coast (Tschudy, 1973b).

Choanopollenites conspicuus (Groot & Groot 1962) Tschudy 1973

Plate 4, figure 1

Latipollis conspicuus Groot and Groot, 1962, p. 169, pl. 30, fig. 35-36; pl. 31, fig. 1-3.

Extratropipollenites conspicuus (Groot & Groot) Srivastava, 1972, p. 252, pl. 13, fig. 4.

Choanopollenites conspicuus (Groot & Groot) Tschudy, 1973b, p. C10-C11, pl. 8, fig. 1-16; Text-Figure 10; Frederiksen, 1979, p. 156, pl. 3, fig. 13.

Dimensions. Equatorial diameter 38 – 40 μm (two specimens measured). Groot and Groot (1962) gave a measurement of 55 μm for the holotype. Tschudy (1973b) gave a range of 35 - 57 μm with an average of 46 μm for his specimens from the US Gulf Coast. My specimens are therefore at the smaller end of the size range of this species.

Remarks. *Choanopollenites conspicuus* represents large grains with a concave-triangular amb. The apices are rounded and the surface of the grain is psilate to scabrate. This species can be distinguished from *Choanopollenites patricius* by its concave-triangular shape and thinner and more delicate nexinal flaps around the endogerminal. *Choanopollenites eximius* is generally larger than *Choanopollenites conspicuus*, and has straighter sides and more angular apices. Other species of *Choanopollenites* are smaller.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <0.4% in 3/151 samples, from the Porters Creek to the Tusahoma formations on the eastern Gulf Coast.

Choanopollenites discipulus Tschudy 1973

Plate 4, figure 2

Choanopollenites discipulus Tschudy, 1973b, p. C9-C10, pl. 7, fig. 1-14; Text-Figure 9.

Dimensions. Equatorial diameter 24 – 25 μm (three specimens measured) Tschudy (1973b) gave a range of 24 – 34 μm for the protologue specimens.

Remarks. *Choanopollenites discipulus* represents mid-sized *Choanopollenites*-type pollen. The amb is concave-triangular, and the exine is smooth around the germinals and scabrate to weakly verrucate elsewhere. The nexine is thicker at the germinals than in the interapertural area, and forms pointed triangular flaps about the endogerminal. This species is most similar to *Choanopollenites conspicuus* but is distinguished by its smaller size, relatively thicker nexine around the germinals, and a slightly coarser sculpturing in the interapertural and polar areas.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 4/151 samples, from the Porters Creek Formation only. This species has also been recorded from the underlying Clayton Formation (Tschudy, 1973b).

Choanopollenites patricius Tschudy 1973

Plate 4, figure 3

Choanopollenites patricius Tschudy, 1973b, p. C12, pl. 9, fig. 1-11; Text-Figure 11.

Dimensions. Equatorial diameter 34 – 45 μm , mean 38 μm (three specimens measured). Tschudy (1973b) gave a range of 39 – 47 μm for the protologue specimens.

Remarks. *Choanopollenites patricius* is medium sized for this genus, and has a rounded triangular amb. It is distinguished by distinct nexinal thickenings adjacent to the endogerminal, at which point the nexine pulls away from the sexine to produce a narrow vestibulum. The nexinal flaps that form the endogerminal are reflexed inwards in equatorial view towards the grain centre. The most similar

species to *Choanopollenites patricius* in terms of overall amb shape is *Choanopollenites consanguineus* Tschudy 1973, but this latter taxon is about half the size of *Choanopollenites patricius*, and lacks the distinctly thickened nexine around the endogerminal.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <3% in 2/151 samples, from the Nanafalia Formation only. This species appears to be limited to this formation (Tschudy, 1973b).

Choanopollenites sp. cf. *Choanopollenites eximius* Stover in Stover et al 1966

Plate 4, figure 4

Dimensions. Equatorial diameter 49 – 58 μm (two specimens measured). Stover (in Stover et al., 1966) gave a range of 71 to 82 μm for *Choanopollenites eximius*.

Remarks. *Choanopollenites eximius* (Stover in Stover et al., 1966, p. 8, pl. 4, fig. 1) is very large for this genus, and the amb is triangular with straighter sides than is found in most other *Choanopollenites* morphotypes. Slightly bulging germinal areas do result in a slight concavity to the amb shape, however. The exine is smooth to punctate or scabrate, and the grain is marked by a poorly defined triradiate area of lighter exine that connects the apical areas across the pole. This feature helps to differentiate *Choanopollenites eximius* from *Choanopollenites conspicuus*, along with less prominent germinal areas in the former species, which result in more angular apices. *Choanopollenites eximius*, as described by Stover (in Stover et al., 1966), is also distinctly larger than *Choanopollenites conspicuus*. Specimens I have assigned to *Choanopollenites* sp. cf. *C. eximius* fall well below the size range given by Stover (in Stover et al., 1966) for *Choanopollenites eximius*, and occupy the upper end of that occupied by *Choanopollenites conspicuus*. However, my specimens match well the description of *Choanopollenites eximius* in terms of amb shape, the more angular

nature of the apices, and the presence of a triradiate structure of different colouration. I have therefore tentatively associated my specimens with *Choanopollenites eximius*.

Botanical affinity. Unknown.

Occurrence. Two specimens found in samples from the Calvert Bluff Formation in Texas. *Choanopollenites eximius* has previously only been recorded from the Late Paleocene of Texas and not from the eastern Gulf Coast, suggesting a limited geographic range for the parent plant species. This taxon may also be a useful Late Paleocene biostratigraphic marker taxon in Texas.

Genus *Complexiopollis* (Krutzsch 1959) Tschudy 1973

Type species. *Complexiopollis praeatumesceus* Krutzsch 1959.

Remarks. Pollen of this Normapollen genus is triangular to concave-triangular with elongated apices in polar view, and triplanoid to triplane in equatorial view. The exine is thin; the sexine and nexine are of a similar thickness but may be hard to distinguish from one another. Tschudy (1973b) emended Krutzsch's (1959b) original diagnosis to include forms with thread-like nexinal arcs, as displayed by morphotypes from the US Gulf Coast. Some species may owe their rigid triplane shape to these arcs (Tschudy, 1973b). As with *Choanopollenites* the exogerminal in *Complexiopollis* is formed by a longitudinal slit in the sexine at the grain apices, and is marked by radially projecting bacula from the inner layer of the sexine. A vestibulum is also present. The nexinal aperture is more complex than in *Choanopollenites*, comprising a longitudinal mesogerminal arranged perpendicular to the exogerminal (= the endogerminal in *Choanopollenites*), and an atriate endogerminal formed by the inner layer of the nexine. *Choanopollenites* further differs from *Complexiopollis* in having a thicker exine in which the sexine is distinctly thicker than the nexine, and in being oval in equatorial view rather than triplane rhomboidal.

Complexiopollis spp.

Plate 4, figures 5-6

Dimensions. Equatorial diameter 26 – 32 μm , mean 30 μm ; polar diameter 18 – 22 μm , mean 19 μm (six specimens measured).

Remarks. Pollen assigned to *Complexiopollis* spp. are similar to Tschudy's (1973b) species *Complexiopollis patulus* and *Complexiopollis microverrucosus*. The former species is recognised by its incomplete arci and indistinct sculpture, the latter by its more prominent baculate areas and arci, and by its finely verrucate sculpture. Both taxa are of a similar size (*Complexiopollis patulus* is 24 – 37 μm in equatorial diameter; *Complexiopollis microverrucosus* is 25 – 39 μm (Tschudy, 1973b)) and are triplane rhomboidal in equatorial view (in which the majority of specimens were observed). Despite the similarity to these taxa, specimens I have assigned to *Complexiopollis* spp. do show variation in terms of arci style and overall grain shape. I have not assigned these specimens below genus level because (a) the specimens recovered appear to intergrade morphologically and were hard to separate into discrete morphological groups, (b) diagnostic features such as the incomplete arci in *Complexiopollis patulus* were often not possible to observe, meaning that these individuals could not be reliably assigned to a form-species, and (c) species of *Complexiopollis* have previously only been recorded from the Cretaceous of the US Gulf Coast (Tschudy, 1973b), suggesting that the specimens in my material may be reworked.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <4% in 27/151 samples, from the Porters Creek Formation to the Meridian Sand Member of the Tallahatta Formation on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Interpollis* Krutzsch 1960

Type species. *Interpollis supplingensis* (Pflug in Thomson & Pflug 1953) Krutzsch 1960.

Remarks. In this Normapolle genus the pollen grains are constricted about the equator, giving a double lense-shape to the grain. The amb at the equator is triangular to concave triangular; the subequatorial outline is weakly concave triangular to convex triangular. The other distinguishing feature of this genus is the presence of six exopores, which are positioned subequatorially at the angles of the grain, three on the proximal face and three on the distal face. There are three equatorial endopores, one at each angle, which may be atriate. The nexine and sexine are of a similar thickness, and may be separated by a narrow interloculum. The grain surface is at most only weakly sculptured.

Interpollis microsupplingensis Krutzsch 1961

Plate 4, figures 7-8

Interpollis microsupplingensis Krutzsch, 1961, p. 305, pl. 1, fig. 12-23; Tschudy, 1975, p. 12, pl. 4, fig. 22-25; Frederiksen, 1979, p. 158, pl. 3, fig. 30; Frederiksen, 1980b, p. 160, pl. 2, fig. 7; Harrington, 2003b, pl. 1, figs. 7-9.

Dimensions. Equatorial diameter 17 μm , subequatorial diameter 20 μm (one specimen measured). Krutzsch (1961) gave a range of 10 – 20 μm for the protologue specimens.

Remarks. This taxon describes small grains with a distinct equatorial constriction. The equatorial outline is concave-triangular and the subequatorial outline is triangular with nearly straight sides. The six exopores are small and circular and 1 – 2 μm in diameter. The exine is shagrenate to punctate. This taxon differs from *Interpollis paleocenica* (Elsik 1968) Frederiksen 1980 in being smaller, having a distinct

equatorial constriction, and lacking an interloculum.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1.1% in 8/151 samples, from the Hatchetigbee to the Tallahatta formations on the eastern Gulf Coast. This appears to represent the true range of this taxon on the US Gulf Coast (Tschudy, 1975).

Interpollis paleocenica (Elsik 1968) Frederiksen 1980

Plate 4, figure 9

Thomsonipollis paleocenicus Elsik, 1968b, p. 614-616, pl. 16, fig. 1-2.

Interpollis intranodus Tschudy, 1975, p. 12, pl. 5, fig. 1-15; Text-Figure 7.

Interpollis paleocenica (Elsik) Frederiksen, 1980b, p. 160, pl. 2, fig. 8.

Dimensions. Equatorial diameter 25 – 29 μm (two measured specimens). Elsik (1968b) gave a range of 30 – 35 μm for the protologue specimens. Tschudy (1975) gave a range of 20 – 36 μm for *Interpollis intranodus*, which is synonymous with *Interpollis paleocenica*, according to Frederiksen (1980b).

Remarks. This species of *Interpollis* is not obviously constricted about the equator, but shows the same arrangement of six subequatorial exopores and three equatorial endopores diagnostic of this genus. The exopores are in the form of lalongate slits. The endopores are indistinct in polar view, but at the grain angles the nexine is pulled away from the sexine to form a vestibulum. The exine is tectate-columellate; the columellae are distinct in well-preserved specimens (the peg-like bacula within the interloculum noted by Tschudy (1975)), and are sparsely distributed across the grain, except in the polar areas where they are absent. The polar areas frequently show a triangular exinal fold. *Interpollis paleocenica* is similar to *Interpollis supplingensis* (Pflug in Thomson & Pflug 1953) Krutzsch 1961, but the latter species has a distinct equatorial constriction, and much finer and more closely spaced columellae.

Botanical affinity. Unknown.

Occurrence. Two specimens observed in the Naheola Formation. This taxon has previously been recorded as ranging down into the latest Cretaceous Owl Creek Formation on the eastern Gulf Coast (Tschudy, 1975), and in the latest Paleocene of Texas (Elsik, 1968b).

Genus *Kyandopollenites* Stover in Stover et al. 1966

Type species. *Kyandopollenites anneratus* Stover in Stover et al. 1966.

Remarks. This distinctive, monotypic Normapollen genus is characterised by its large size, circular amb, annulate pores, thick exine, and granulate sculpture. The sexine is thicker than the nexine and is stratified into a thicker ectosexine that thickens at the pore to form the annulus, and a thinner endosexine that thins near the pore. *Kyandopollenites* differs from *Emscheripollis* Krutzsch 1959 and *Papillopollis* Pflug 1953 in having more convex sides, slightly annulate apertures and less clearly differentiated wall layers. *Emscheripollis* also has tori and *Papillopollis* has vestibulate apertures, neither of which are features of *Kyandopollenites*.

Kyandopollenites anneratus Stover in Stover et al. 1966

Plate 4, figure 10

Kyandopollenites anneratus Stover in Stover et al., 1966, p. 6-7, pl. 3, figs. 1-2; Tschudy, 1973a, p. B9, B13, pl. 1, fig. 3-4; Tschudy, 1975, p.13, pl. 7, fig. 1-5; Text-Figure 9; Frederiksen, 1979, p. 158.

Dimensions. Equatorial diameter 43 μm (one specimen measured). Stover (in Stover et al., 1966) gave a range of 47.5 – 54 μm for the protologue specimens; Tschudy (1975) increased this to 41 – 58 μm .

Remarks. The morphology of this species has already been described in the genus remarks. The exine was 5 μm thick in the interapertural areas on my measured specimen, and thickened to nearly 8 μm at the apertures, which agrees well with Stover's (in Stover et al., 1966) measurements.

Botanical affinity. Unknown.

Occurrence. Two specimens observed in the Tuscaloosa Formation. Based on its range base in Virginia, Frederiksen (1998) suggested that this taxon has its first appearance in the upper part of the Tuscaloosa Formation, making it a useful marker taxon to differentiate the Tuscaloosa and underlying Nanafalia formations. This is inconsistent with Tschudy (1973a), who recorded *Kyandopollenites anneratus* as being present in the Nanafalia Formation as well. This morphotype was first described from the Wilcox Group of Texas (Stover in Stover et al., 1966), although I did not recover any specimens from the Calvert Bluff Formation.

Genus *Momipites* Wodehouse 1933 emend. Nichols 1973

Type species. *Momipites coryloides* Wodehouse 1933.

Remarks. This genus was emended by Nichols (1973) to accommodate juglandaceous pollen morphologically related to the Engelhardioideae. The grains are triporate, and have atriate but otherwise simple pores. Only weak annuli or tumescences are ever present. The exine is smooth to evenly granulate. Some taxa show polar modifications of the exine, such as thinned areas of varying shapes, triradiate thickenings, or folds. Circumpolar rings of thinned exine are reminiscent of modern *Carya* pollen, but in *Momipites* the pores are always located on the equator rather than being displaced onto one hemisphere. Folds may be shaped in such a way as to be suggestive of modern *Platycarya* pollen, but true pseudocolpi are not present. Apart from exinal modifications, individual species are distinguished based on the

size and shape of the amb (Nichols and Ott, 1978). These features have also been used to group species of *Momipites* into informal groups (Nichols, 1973; Frederiksen and Christopher, 1978). Some tropical *Momipites* species have been associated with the Moraceae (Jaramillo et al., 2010).

Frederiksen and Christopher (1978) further emended this genus to exclude forms with triradiate folds or thickenings, and/or multiple thin spots. These they assigned to *Plicatopollis* Krutzsch 1962 emend. Frederiksen & Christopher 1978, reasoning that “the genus *Momipites* is too heterogeneous if species of these groups are included in it” (Frederiksen and Christopher, 1978; p. 124). However, given the acknowledged close morphological relationship between *Momipites* and *Plicatopollis* (Frederiksen and Christopher, 1978), there seems to be little value in maintaining two genera of *Momipites*-type pollen, especially given the uncertainty over the nature of the triradiate structure in North America *Plicatopollis* types (see Frederiksen and Christopher, 1978; Frederiksen, 1979). I therefore reject Frederiksen and Christopher’s (1978) emendation of this genus, and instead follow that of Nichols (1973), which adequately incorporates the morphological variability observed in published records of *Momipites*. See further discussion under *Momipites triradiatus* and *Momipites ventifluminis*.

Momipites anellus Nichols & Ott 1978

Plate 4, figure 11

Momipites anellus Nichols and Ott, 1978, p. 103, pl. 1, fig. 22-25; Jardine and Harrington, 2008, pl. 2, fig. 8.

Dimensions. Equatorial diameter 22 – 28 μm , mean 26 μm (five specimens measured). Nichols and Ott (1978) gave a range of 18 – 27 μm for the protologue specimens.

Remarks. This species of *Momipites* has a convex outline, and a *Carya*-style circumpolar ring of thinned exine at one pole, which surrounds a polar island of normal exine thickness. The pores are atriate and slightly tumescent, and the exine is evenly granulate. This species falls into the *Momipites tenuipolus* Group of Nichols (1973) and Frederiksen and Christopher (1978), which is circumscribed by the presence of a ring of thinned exine about one pole. It differs from other members of this group mainly by size: *Momipites anellus* is larger than *Momipites tenuipolus* Anderson 1960, and shows a more prominent polar island of normal exine thickness, and is smaller than *Momipites amplus* (Leffingwell 1971) Nichols 1973. *Momipites marylandicus* (Groot & Groot 1962) Nichols 1973 occupies the lower end of the size range of *Momipites anellus*, and is otherwise similar to this species. *Momipites leffingwellii* Nichols & Ott 1978 has concave sides. Since all of my specimens are close to the size range of *Momipites anellus*, I have used this form species rather than assigning my specimens to the *Momipites tenuipolus* Group. *Momipites anellus* differs from *Momipites nicholsii* in having a round, rather than polygonal circumpolar ring, and in only having a ring at one pole, rather than at both.

Botanical affinity. Juglandaceae.

Occurrence. Occurred in relative abundances of <1.5% in 43/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Momipites coryloides Wodehouse 1933

Plate 4, figure 12

Momipites coryloides Wodehouse, 1933, p. 511, fig. 43; Wilson and Webster, 1946, p. 275-276, fig. 15; Frederiksen and Christopher, 1978, p. 128-129, pl.1, fig. 1; Frederiksen, 1979, p. 144; Frederiksen, 1980a, p. 38-39, pl. 7, fig. 12-14; Jardine and Harrington, 2008, pl.

2, fig. 6.

Triatripollenites sp. of the *T. coryphaeus* type (20 μ –30 μ Tschudy, 1973a, p. B16, pl. 4, fig. 12-13.

Momipites wyomingensis Nichols & Ott, 1978. Jardine and Harrington, 2008, pl. 2, fig. 7.

Dimensions. 24 – 29 μ m, mean 26 μ m (13 specimens measured). Wodehouse (1933) gave a range of 21 – 33 μ m for the protologue specimens.

Remarks. *Momipites coryloides* accommodates pollen of the basic Engelhardioideae type. The amb is triangular with convex sides, the exine is slightly tumescent at the pores, and there are no modifications to the exine at the pole. *Momipites microfoveolatus* differs in being smaller and having a more variable amb shape, *Momipites strictus* differs in having straight sides, and *Momipites waltmanensis* differs in having distinctly concave sides. I have not recognised *Momipites wyomingensis* Nichols & Ott 1978 in my counts because (a) the size range overlaps extensively with *Momipites coryloides*, so specimens with convex interporia are adequately accommodated there, and (b) *Momipites wyomingensis* types with more or less straight sides (e.g. Pocknall and Nichols, 1996; pl. 7, fig. 2-3) are better incorporated into *Momipites strictus*, which is distinguished by this particular amb shape. Nichols (2010) has also stated that *Momipites coryloides* and *Momipites wyomingensis* may be conspecific.

Botanical affinity. Juglandaceae, possibly Engelhardioideae (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <13% in 94/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. On the Gulf Coast this species is known to range up into at least the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Momipites microfoveolatus (Stanley 1965) Nichols 1973

Plate 4, figure 13

Engelhardtia microfoveolata Stanley, 1965, p. 300-301, pl. 45, fig. 3-13.

Momipites microfoveolatus (Stanley) Nichols, 1973, p. 107; Frederiksen and Christopher, 1978, p. 130, pl. 1, fig. 7-10; Frederiksen, 1979, p. 142, pl. 1, fig. 18; Frederiksen, 1980a, p. 39, pl. 7, fig. 15-16; Frederiksen in Frederiksen et al., 1983, p. 33-34, pl. 8, fig. 16-17.

Triatriopollenites sp. of the *T. coryphaeus* type (13 μ -18 μ) Tschudy, 1973a, p. B16, pl. 4, fig. 1-3.

Dimensions. Equatorial diameter 16 – 21 μ m, mean 18 μ m (15 measured specimens). Stanley (1965) gave a range of 15 – 22 μ m for the protologue specimens.

Remarks. *Momipites microfoveolatus* is small, has a slightly convex- to slightly concave-triangular amb, very little sexinal thickening at the pores, and no exinal modification at the pole. The sexine is infra-granulate (Frederiksen, 1980a). Most grains in my material had convex or straight sides. As with *Momipites coryloides* this species represents basic *Momipites*-type pollen; the two taxa differ mainly in size, although more variation in amb shape is accommodated under *Momipites microfoveolatus*. *Momipites inaequalis* Anderson 1960 is similar to *Momipites microfoveolatus*, except in that the sides in the former species are of unequal length.

Botanical affinity. Juglandaceae, possibly Engelhardioideae (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <6% in 83/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. On the Gulf Coast this species is known to range up into at least the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Momipites nicholsii Frederiksen 1998

Plate 4, figure 14

Momipites tenuipolus group (in part). Frederiksen, 1979, pl. 1, fig. 23-27.

Momipites-Plicatopollis-Platycaryapollenites complex (in part). Frederiksen, 1979, pl. 2, fig. 13 only.

Momipites tenuipolus group (*Platycaryapollenites* type) (in part). Frederiksen, 1988, pl. 2, fig. 23-24 only.

Momipites nicholsii Frederiksen, 1998, p. 62, 66, pl. 1, fig. 5-9.

Dimensions. Equatorial diameter 24 – 25 μm (three specimens measured).

Frederiksen (1998) gave a range of 19 – 30 μm for the protologue specimens.

Remarks. *Momipites nicholsii* is characterized by an irregularly polygonal ring of thin exine at each pole, surrounding a polar island of normal exine thickness. The amb is convex triangular and the sexine may be slightly annulate at the pores. The atria are not prominent due to the thinness of the nexine. This morphotype differs from *Momipites anellus*, and other members of the *Momipites tenuipolus* Group, by the presence of circumpolar rings at both poles, and the polygonal, rather than circular, shape of the rings. Frederiksen (1998) suggested that the polygonal rings of *Momipites nicholsii* were derived from pseudocolpi of *Platycaryapollenites*-type pollen, demonstrating the morphological continuity between these Palaeogene juglandaceous forms.

Botanical affinity. Juglandaceae, possibly Engelhardioideae (Frederiksen, 1998).

Occurrence. Occurred in relative abundances of <1.3% in 4/151 samples, in the Tallahatta Formation only. This species is known to range down into the Hatchetigbee Formation on the eastern Gulf Coast, and one similar specimen has been recorded from the Tusahoma Formation (Frederiksen, 1998).

Momipites strictus Frederiksen & Christopher 1978

Plate 4, figure 15

Engelhardtia inaequalis (Anderson 1960) Elsik, 1968b [misidentified], p. 602, pl. 16, figs. 17, 19-20.

Momipites strictus Frederiksen and Christopher, 1978, p. 129, pl. 1, figs. 2-6;
Frederiksen, 1979, p. 144, 146.

Dimensions. Equatorial diameter 25 – 28 μm , mean 27 μm (four specimens measured). Frederiksen and Christopher (1978) gave a range of 23 – 32 μm for the protologue specimens.

Remarks. This species has a triangular amb with more or less straight sides. In most specimens the sexine is slightly tumescent at the pores. An area of slightly thinner exine is often observed at one pole, but there is no polar island of normal exine thickness, as is found in *Momipites anellus*. This species differs from *Momipites coryloides* and *Momipites waltmanensis* in having straight sides; in the former species the sides are convex, and in the latter species they are concave. *Momipites inaequalis* Anderson 1960 is smaller, and has sides of different lengths.

Botanical affinity. Juglandaceae.

Occurrence. Occurred in relative abundances of <7% in 55/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. *Momipites strictus* is an important Paleocene marker taxon on the US Gulf Coast (Frederiksen and Christopher, 1978; Frederiksen, 1998).

Momipites triradiatus type

Plate 4, figure 16

Engelhardtia quietus (Potonié 1934) Elsik, 1968b, p. 600, 602, pl. 16, fig. 7, 9-16, 18.

Momipites triradiatus Nichols, 1973, p. 108, pl. 1, fig. 10-15.

Triatriopollenites quietus (Potonié 1934) Thomson and Pflug, 1953. Tschudy, 1973a, p. B12. pl. 1, fig. 18-20.

Plicatopollis spp. of the *P. plicata* type. Frederiksen and Christopher, 1978, p. 134, pl. 2, fig. 5-8.

Plicatopollis spp. of the *P. lunata* type. Frederiksen and Christopher, 1978, p. 134-135, pl. 2, fig. 9-14, 15-16.

Plicatopollis lunata type Frederiksen, 1979, p. 148-149; Frederiksen, 1980b, p. 153.

Dimensions. Equatorial diameter 23 – 28 μm . Nichols (1973) gave a range of 19 – 25 μm for *Momipites triradiatus*.

Remarks. As circumscribed by Nichols (1973), *Momipites triradiatus* has a triradiate thickening centred over one pole, which radiates out to the apertures. Folds may border this thickening. The amb is convex-triangular and the exine does not show any pronounced thickening at the pores. In addition to transferring this species to *Plicatopollis*, Frederiksen and Christopher (1978) highlighted the variation present in the triradiate structure. It may be formed by thickening or folds, and may be accompanied by three thin spots in the exine of one or both hemispheres. Whilst I do not follow Frederiksen and Christopher's (1978) transfer of this species to *Plicatopollis* (see *Momipites* genus remarks), I do concur with the morphological variability present in the triradiate structure, and the difficulty in assigning these forms to individual species (Frederiksen and Christopher (1978) initially assigned types with triradiate folds (= plicae) to *Plicatopollis* spp. of the *P. plicata* type, and types with triradiate thickenings (= endoplicae) to *Plicatopollis* spp. of the *P. lunata* type, but subsequently Frederiksen (1979, 1980b) included these together under the designation *Plicatopollis lunata* type). I have therefore assigned specimens of this kind to an informal group, which acknowledges the variability in this morphotype beyond *Momipites triradiatus sensu stricto*, while still maintaining the presence of this

morphology under *Momipites*.

Botanical affinity. Juglandaceae (Nichols 1973).

Occurrence. Occurred in relative abundances of <5% in 29/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Momipites ventifluminis Nichols & Ott 1978

Plate 4, figure 17

Momipites ventifluminis Nichols and Ott, 1978, p. 102, pl. 1, fig. 9-14; Pocknall and Nichols, 1996, p. 28-29, pl. 6, fig. 24-25.

Plicatopollis spp. of the *P. triorbicularis* type. Frederiksen and Christopher, 1978, p. 134, pl. 2, fig. 1-4.

Dimensions. Equatorial diameter 26 – 29 μm , mean 28 μm (three specimens measured). Nichols and Ott (1978) gave a range of 21 – 27 μm for the protologue specimens. Pocknall and Nichols (1996) gave a range of 18 – 28 μm for their specimens from the Powder River Basin of Montana and Wyoming.

Remarks. This species of *Momipites* has a convex amb and three spots of thinned exine located around the pole on one hemisphere. My specimens are slightly larger than those described by Nichols and Ott (1978), and possibly represent *Momipites rotundus* (Leffingwell 1971) Nichols 1973, which is similar to *Momipites ventifluminis* but has a size range of 24 – 34 μm . Here I follow Pocknall and Nichols (1996) in including all forms with convex sides and thin spots to *Momipites ventifluminis*. *Momipites triorbicularis* (Leffingwell 1971) Nichols 1973 differs in having a straight sided to concave amb, and in being smaller. In amb shape and size *Momipites ventifluminis* most closely resembles *Momipites coryloides*, but differs in having three thin spots about one pole.

As with *Momipites triradiatus*, Frederiksen and Christopher (1978) considered forms with three thin spots to be better accommodated by *Plicatopollis*. They emphasised the strong morphological links between these forms, especially given the presence of thin spots in some grains with triradiate folds or thickenings. However, there is arguable morphological continuity between *Momipites ventifluminis*, *Momipites coryloides*, and *Momipites anellus* (similar size and convex amb), and between *Momipites triorbicularis*, *Momipites waltmanensis* and *Momipites leffinwellii* Nichols & Ott 1978 (similar size and concave amb) (Nichols and Ott, 1978). Including all such forms in *Momipites* therefore seems justified.

Botanical affinity. Juglandaceae (Pocknall and Nichols, 1996).

Occurrence. Four specimens observed, in the Tuscaloosa, Hatchetigbee and Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon is much more abundant in the Late Paleocene of the Western Interior (Pocknall and Nichols, 1996).

Momipites waltmanensis Nichols & Ott 1978

Plate 4, figure 18

Momipites waltmanensis Nichols and Ott, 1978, p. 102, pl. 1, fig. 5-8; Pocknall and Nichols, 1996, p. 29, pl. 7, fig. 1.

Momipites flexus Frederiksen, 1979, p.142, 144, pl. 1, fig. 19; Frederiksen, 1980b, p. 153.

Dimensions. Equatorial diameter 21 – 31 μm , mean 24 μm (five specimens measured). Nichols and Ott (1978) gave a range of 16 – 25 μm for the protologue specimens.

Remarks. *Momipites waltmanensis* is distinguished from other species of *Momipites* in this study by the presence of concave sides. There is no exinal modification at the pole, and the exine typically shows a slight tumescence towards the pores. Some of

my specimens are slightly larger than Nichols and Ott's (1978), but are otherwise similar. *Momipites flexus* Frederiksen 1979 is nearly identical in terms of amb size and shape, exine thickness and structure, and the morphology of the pores. I therefore consider it to be a junior synonym of *Momipites waltmanensis*. *Momipites coryloides* has convex sides and *Momipites strictus* has straight sides, but these three forms are otherwise similar to each other in terms of size and lack of polar exinal modifications.

Botanical affinity. Juglandaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <1.3% in 26/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

"Momipites cf. M. flexus" of Frederiksen 1998

Plate 4, figure 19

Momipites cf. M. flexus Frederiksen 1979. Frederiksen 1998, pl. 2, fig. 1-4.

Dimensions. Equatorial diameter 24 µm (three specimens measured).

Remarks. This taxon is characterised by the presence of arci running between the pores. The sides of the grain are typically straight to concave, but may be slightly convex. There is little or no thickening of the sexine at the pore. As with other *Momipites* species the exine is granulate and the pores are atriate. This species differs from other *Momipites* species in possessing arci. It differs from *Paraalnipollenites confusus* in lacking false pores and a polar ring of thickened exine, and in having better-developed arci.

Botanical affinity. Probably Juglandaceae.

Occurrence. Occurred in relative abundances of <3% in 17/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Nudopollis* Pflug 1953

Type species. *Nudopollis endangulatus* (Pflug in Thomson & Pflug 1953) Pflug 1953.

Remarks. *Nudopollis* includes *Normapolle*-type pollen with prominent germinals formed by a long annulus. The pollen grain is oblate and convex- to concave-triangular in polar view; the germinals protrude out to a greater or lesser extent at the grain angles. The germinals are usually monannulate, and rarely polyannulate, and are not endannulate or vestibulate. They may be atriate. A mesopore is present, in the form of a basket-like filter. The inner contour is variable in shape among species, from triangular to rounded. The sexine is smooth to chagrinate, and there is no interloculum. Like *Basopollis*, *Choanopollenites* and *Complexiopollis*, the exopore is lolongate and slit-shaped, but unlike these three genera there is no baculate inner layer to the sexine at the apertures. All three genera are also vestibulate.

Nudopollis endangulatus (Pflug in Thomson & Pflug 1953) Pflug 1953

Plate 4, figure 20

Extratropopollenites endangulatus Pflug in Thomson and Pflug, 1953, p. 72, pl. 6, fig. 37-42.

Nudopollis endangulatus (Pflug) Pflug, 1953, p. 108, pl. 25, fig. 24; Frederiksen, 1979, p. 155; Frederiksen, 1980b, p. 171, pl. 4, fig. 9-10.

Nudopollis aff. *N. endangulatus*. Tschudy, 1975, p. 15, pl. 8, fig. 10-11.

Dimensions. Equatorial diameter 23 – 25 μm , mean 24 μm (four measured specimens). Pflug (in Thomson and Pflug, 1953) gave a range of 25 – 35 μm for the protologue specimens.

Remarks. In this species of *Nudopollis* the amb is triangular to concave-triangular, and the inner contour is convex triangular and not circular. The sexine is thicker

than the nexine, and the mesogerminal is poorly developed. One abnormal four-aperturate form was found in the Tusahoma Formation. This species differs from *Nudopollis thiergartii* in having a triangular rather than circular inner contour, and from *Nudopollis terminalis* in having a concave to straight-sided amb, rather than having distinctly convex sides.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 8/151 samples, from the Naheola to the Tusahoma formations on the eastern Gulf Coast.

Nudopollis terminalis (Pflug & Thomson in Thomson & Pflug 1953) Pflug 1953

Plate 4, figure 21

Extratropopollenites terminalis Pflug and Thomson in Thomson and Pflug, 1953, p. 71, pl. 6, fig. 30-36; Srivastava, 1972, p. 254, pl. 14, fig. 5 – 6.

Nudopollis terminalis (Pflug & Thomson) Pflug, 1953, p. 161, pl. 22, fig. 1-6; Elsik, 1968b, p. 648-650, pl. 36, fig. 9-10; Frederiksen, 1979, p. 154-155; Frederiksen, 1980a, p. 62, pl. 15, fig. 23; Harrington, 2003b, pl. 1, fig. 27; Jardine and Harrington, 2008, pl. 2, fig. 9.

Nudopollis spp. of the *N. terminalis* type. Tschudy, 1973a, p. B14, pl. 2, fig. 18-20.

Nudopollis aff. *N. terminalis*. Tschudy, 1975, p. 16, pl. 8, fig. 16-25.

See Elsik (1968b) for further synonymy

Dimensions. Equatorial diameter 24 – 35 μm , mean 30 μm (nine specimens measured). Pflug and Thomson (in Thomson and Pflug, 1953) gave a range of 20 – 40 μm for the protologue specimens.

Remarks. *Nudopollis terminalis* is characterised by a distinctly convex amb, which in some specimens would be subcircular were it not for the protruding germinals,

and a triangular inner contour. The pore canal is conically expanded towards the centre of the grain, shaping the atrium. This species differs from *Nudopollis thiergarti* in having a triangular inner contour and a convex amb. It differs from *Nudopollis endangulatus* in having a convex amb, and by having a triangular inner contour that is offset from the triangular outline of the amb by 60°. In *Nudopollis endangulatus* the two are aligned.

Botanical affinity. Unknown.

Occurrences. Occurred in relative abundances of <17% in 102/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. *Nudopollis terminalis* was by far the most abundant species of *Nudopollis* in this study. It is known to range up into the Late Eocene Jackson Group on the US Gulf Coast (Frederiksen, 1980a).

Nudopollis thiergartii (Thomson & Pflug 1953) Pflug 1953

Plate 4, figure 22

Extratropopollenites thiergarti Thomson and Pflug, 1953, p. 71-72, pl. 6, fig. 43-54, 57-63.

Nudopollis thiergarti (Thomson & Pflug) Pflug, 1953, p. 109, pl. 25, fig. 25-48; Elsik, 1968b, p. 648, pl. 36, fig. 7-8; Frederiksen, 1979, p. 155, pl. 3, fig. 10.

Nudopollis spp. of the *N. thiergarti* type. Tschudy, 1973a, p. B12, pl. 1, fig. 6-7.

Nudopollis aff. *N. thiergartii*. Tschudy, 1975, p. 16, pl. 8, fig. 12-15.

See Elsik (1968b) for further synonymy.

Dimensions. Equatorial diameter 28 µm (one specimen measured) Thomson and Pflug (1953) gave a range of 12 – 35 µm for the protologue specimens.

Remarks. This species is defined by its circular inner contour, which neither of

the other *Nudopollis* species in this study possesses. The amb is convex to weakly concave, and the exine is thin and chagrinate.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 3/151 samples, from the Naheola, Nanafalia and Tallahatta formations on the eastern Gulf Coast. This species is known to range down to the Maastrichtian on the US Gulf Coast (Tschudy, 1975).

Genus *Paraalnipollenites* Hills & Wallace 1969

Type species. *Paraalnipollenites confusus* (Zaklinskaya 1963) Hills & Wallace 1969.

Remarks. This genus describes triporate to occasionally tetraporate pollen with poorly developed arci, which frequently swing out to form a false pore midway between the true pores. The true pores are at the apices of the grain, and may be labrate but never vestibulate. The amb is triangular with convex to straight sides, and the exine is finely granulate. This genus differs from *Jarzenipollenites* Kedves 1980 and *Alnipollenites* Potonié 1931 in having false pores and poorly developed arci; the latter genus is defined by its vestibulate pores.

Paraalnipollenites confusus (Zaklinskaya 1963) Hills & Wallace 1969

Plate 4, figure 23

Triatriopollenites confuses Zaklinskaya, 1963, p. 232, pl. 34, fig. 7.

Paraalnipollenites confusus (Zaklinskaya) Hills and Wallace, 1969, p. 141; Frederiksen, 1988, pl. 3, fig. 16.

Paraalnipollenites sp. cf. *P. confusus*. Pocknall and Nichols, 1996, p. 29-30, pl. 7, fig. 4-5.

Dimensions. Equatorial diameter 22 – 28 µm (two specimens measured). Hills and

Wallace (1969) gave a range of 22 – 32 μm for specimens of this species from Canada; Zaklinskaya (1963) gave a range of 30 – 40 μm for specimens from the former USSR.

Remarks. The major morphological features of this species have already been described in the genus remarks, excepting the circumpolar ring of thickened exine that sometimes forms on one hemisphere. This ring is most clearly developed when the arci are suppressed. My specimens showed great variability in the size of the labra (if present), the presence of a polar ring, and the extent of the development of arci and false pores. This species is most similar to *Alnipollenites scoticus*, but differs in the presence of false pores, the smaller number of true pores, and the fact that these pores are not vestibulate.

Botanical affinity. Unknown. Pocknall and Nichols (1996) suggested a possible betulaceous affinity for this species, but acknowledged the differing pore structure between this species and Betulaceae.

Occurrence. Occurred in relative abundances of <4% in 9/151 samples, from the Naheola and Hatchetigbee formations on the eastern Gulf Coast. This species is known to range up into the Tallahatta Formation (Frederiksen, 1988).

Genus *Pistillipollenites* Rouse 1962

Type species. *Pistillipollenites mcgregorii* Rouse 1962.

Remarks. This monotypic genus is characterised by a gemmate sculpture and a circular amb. The gemmae are variable in size, shape and distribution, but typically cluster at the pores. The pores themselves are poorly defined and obscured by the gemmae. This genus differs from *Bagelopolis* Carroll 1999 by having a gemmate, rather than verrucate, ornamentation, and by having apertures bordered by gemmae, rather than surrounded by striate 'pseudo-annuli'.

Pistillipollenites mcgregorii Rouse 1962

Plate 5, figures 1-2

Pistillipollenites mcgregorii Rouse, 1962, p. 206, pl. 1, fig. 8-12; emend. Elsik, 1968b, p. 638-640, pl. 34, fig. 9; pl. 35, fig. 1-3; Tschudy, 1973a, p. B14, pl. 2, fig. 21-22; Frederiksen, 1979, p. 154, pl. 3, fig. 5; Frederiksen, 1980b, p. 156, pl. 1, fig. 31; Pocknall and Nichols, 1996, p. 30, pl. 7, fig. 6; Jardine and Harrington, 2008, pl. 2, fig. 15.

Dimensions. Equatorial diameter 21 – 24 μm , mean 22 μm (three specimens measured). Rouse (1962) gave a range of 20 – 30 μm for the protologue specimens.

Remarks. The defining features of this distinctive species have been outlined in the genus remarks. The gemmae vary from grain to grain in terms of size, shape and distribution. The apertures are usually bordered by at least two gemmae. The exine between the gemmae appears psilate but under high magnification is punctate-reticulate (Rouse and Srivastava, 1970). Concentrated bands of gemmae running from aperture to aperture across the pole, as noted by Elsik (1968b), were seen but not prevalent in my material. In my specimens the gemmae varied in diameter from 1 to 4 μm .

Botanical affinity. Crepet and Daghljan (1981) recovered *Pistillipollenites mcgregorii* from gentianaceous flowers from the Wilcox Group of Texas.

Occurrence. Occurred in relative abundances of <3.3% in 50/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Platycarya* Siebold & Zuccarini

Remarks. I have assigned to this genus pollen that has sufficient similarity to that of

extant *Platycarya* to make the use of a form genus unnecessary. In the modern grains two long, narrow pseudocolpi are normally present on each hemisphere, and are mainly formed by thinning of the sexine (Frederiksen and Christopher, 1978). The use of the extant genus is further justified by the discovery of similar pollen types in close association with leaves, fruits and inflorescences that can be confidently assigned to *Platycarya* (Wing and Hickey, 1984). Pollen grains that are pseudocolpate but depart in some way from the morphology of the extant genus were assigned to *Platycaryapollenites*.

Platycarya platycaryoides (Roche 1969) Frederiksen & Christopher 1978

Plate 5, figure 3

Triatriopollenites platycaryoides Roche, 1969, p. 135, text-fig. 6 – 7, pl. 1, fig. 19.

Platycarya spp. Tschudy, 1973a, p. B14-B15, pl. 2, fig. 30-31 only.

Platycarya platycaryoides (Roche) Frederiksen and Christopher, 1978, p. 138, pl. 3, fig. 3 – 6; Frederiksen, 1979, p. 149, pl. 1, fig. 39; Frederiksen, 1998, pl. 1, fig. 14 – 16; Harrington, 2003b, pl. 1, fig. 11.

Platycarya sp. Frederiksen, 1980a, p. 39, pl. 7, fig. 17.

See Frederiksen and Christopher (1978) for further synonymy.

Dimensions. Equatorial diameter 17 – 23 μm , mean 20 μm (three specimens measured). Frederiksen and Christopher (1978) gave a range of 14 – 30 μm , with most specimens being under 24 μm .

Remarks. This taxon includes pollen with a convex-triangular amb, exine $\sim 1\ \mu\text{m}$ thick and faintly granulate, and with two pseudocolpi on each hemisphere. The pseudocolpi are 1-2 μm wide, and on each hemisphere one pseudocolpi may be longer than the other, extending right across the hemisphere and possibly over the

equator. The pores are atriate, and there is little or no annulus or tumescence present. This species is very similar to modern *Platycarya* pollen, apart from its slightly larger size. *Platycarya platycaryoides* can be distinguished from specimens assigned to *Platycaryapollenites* by the consistent number, shape and size of the pseudocolpi.

Botanical affinity. *Platycarya*, Juglandaceae (Frederiksen and Christopher, 1978)

Occurrence. Occurred in relative abundances of <3% in 17/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast. This species is known to range to the top of the Claiborne Group (Middle Eocene) on the US Gulf Coast (Frederiksen, 1980a, 1988).

Genus *Platycaryapollenites* Nagy 1969 emend. Frederiksen & Christopher 1978

Type species. *Platycaryapollenites miocaenicus* Nagy 1969.

Remarks. This form genus includes specimens that show a general resemblance to modern *Platycarya* pollen, but differ in the specific details of the pseudocolpi (e.g. shape, size positioning, and number), and the presence of accompanying exinal folds. As with other juglandaceous pollen the pores are atriate, and in this genus distinct annuli or labra are lacking. *Platycaryapollenites* differs from *Momipites* in showing distinct pseudocolpi, although the two genera intergrade to some extent, partly via *Momipites nicholsii* types, and partly via grains that are similar to *Momipites triradiatus*, but have more irregular or asymmetrical exinal folding and show accompanying pseudocolpi (illustrated as *Plicatopollis/Platycaryapollenites* spp. by Frederiksen, 1998, pl. 1, fig. 23-33).

Platycaryapollenites spp.

Plate 5, figures 4-5

Platycarya spp. Tschudy, 1973a, p. B14-B15, pl. 2, fig. 32-34 only.

Platycaryapollenites spp. Frederiksen, 1998, pl. 1, fig. 19-21.

Dimensions. Equatorial diameter 14 – 25 μm , mean 21 μm (eight specimens measured).

Remarks. Frederiksen (1979, 1998) demonstrated that pollen types broadly corresponding to *Platycaryapollenites* from the Early Eocene of the US Gulf Coast show a range of intergrading morphologies, especially in pseudocolpi shape and arrangement on the grain. The published species *Platycaryapollenites swasticoidus* (Elsik 1974) Frederiksen & Christopher 1978 and *Platycaryapollenites triplicatus* (Elsik 1974) Frederiksen & Christopher 1978 are both variable in shape and intergrade morphologically (Frederiksen, 1979), and similar types with more irregular pseudocolpi have not been assigned to form species (e.g. Frederiksen, 1998). My specimens show much of the variability of these illustrated forms, and in practice it was hard to separate them consistently. I have therefore included them all in one heterogeneous, but clearly delimited, taxon. See Frederiksen (1998, p. 54-55) for further discussion of the possible phylogenetic relationships between *Momipites*, *Platycarya* and *Platycaryapollenites* species on the US Gulf Coast.

Botanical affinity. Juglandaceae (Frederiksen, 1998).

Occurrence. Occurred in relative abundances of <5.1% in 14/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast.

Genus *Pseudoplicapollis* Krutzsch in Góczán et al. 1967

Type species. *Pseudoplicapollis palaeocaenicus* Krutzsch in Góczán et al. 1967.

Remarks. This Normapolle genus includes grains that have plicae connecting the germinals across the poles on each hemisphere. The amb is triangular to convex-

triangular, and in equatorial view the grain is oblate. The exine is thin and smooth to weakly microsculptured, and no interloculum is present. The germinals are at the grain angles and are annulate and may be vestibulate. A thin layer of baculae may line the inner wall of the sexine at the germinals, but this is much less distinct than in *Basopollis* or *Choanopollenites*. The plicae terminate with triangular tips within the germinals, forming the floor of the vestibulum. The exogerminals occur as lalongate equatorial slits, and the endogerminals occur as lalongate slits between the triangular tips of the plicae where they meet at the grain angles. This genus differs from most other Normapollen pollen by having prominent plicae. *Plicapollis* Pflug 1953 emend. Tschudy 1975 also has plicae, but these terminate at the base of the vestibulum rather than in it, and do not terminate in pointed flaps.

Pseudoplicapollis limitata Frederiksen 1978

Plate 5, figure 6

Pseudoplicapollis sp.A Tschudy, 1975, p. 22-23, pl. 13, fig. 13-17; Text-Figure 22.

Pseudoplicapollis limitata Frederiksen, 1978, p. 693-694, fig. 1f-k; Frederiksen, 1979, p. 156-157; Jardine and Harrington, 2008, pl. 2, fig. 13.

Dimensions. Equatorial diameter 27 – 29 μm (two specimens measured). Frederiksen (1978) gave a range of 21 – 36 μm for the protologue specimens.

Remarks. This species includes larger forms of *Pseudoplicapollis* with a triangular to slightly convex-triangular amb, and thin granulate to microverrucate columellate exine. The plicae are relatively narrow and have rounded rather than the pointed ends usually seen in this genus. This taxon may show an indistinct atrium or a deep vestibulum, and an annulus is present at the pores. This taxon differs from *Pseudoplicapollis endocuspis* Tschudy 1975 and *Pseudoplicapollis serenus* in being larger and having relatively narrower plicae with rounded ends.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1.2% in 16/151 samples, from the Porters Creek to the Tuscahoma formations on the eastern Gulf Coast.

Pseudoplicapollis serenus Tschudy 1975

Plate 5, figures 7-8

Pseudoplicapollis serenus Tschudy, 1975, p. 22, Pl. 13, fig. 8-12; Text-Figure 21;
Frederiksen, 1980b, p. 171-172, pl. 4, fig. 2-3.

Dimensions. Equatorial diameter 21 – 24 μm (two specimens measured). Tschudy (1975) gave a range of 13.5 – 19 μm for the protologue specimens.

Remarks. *Pseudoplicapollis serenus* is characterised by blunt germinal regions and prominent vestibula. In polar view each vestibulum appears as two oval chambers, one on either side of the triangular plica tip. The amb is convex-triangular, and the exine is smooth. The pores are distinctly annulate. The plicae in this species are delicate, and Frederiksen (1980b) recorded both plicate and non-plicate (= *Minorpollis* aff. *M. minimus* of Tschudy 1975) forms in the same samples, which he considered to be variants of *Pseudoplicapollis serenus*. Both of the two specimens found in my samples were poorly preserved; one showed weak plicae, and the other was obscured to the extent that it was not possible to determine whether plicae were present or not. This species differs from *Pseudoplicapollis endocuspis* Tschudy 1975 in having blunt, rather than pointed angles, and by the double-oval shape of its vestibulum. In *Pseudoplicapollis endocuspis* the vestibulum is narrow and in the shape of an inverted 'V'.

Botanical affinity. Unknown.

Occurrence. Two specimens recorded from the Porters Creek Formation on the eastern Gulf Coast. This taxon is known to range down to the Campanian (Tschudy,

1975).

Genus *Thomsonipollis* Krutzsch 1960 non Elsik 1968

Type species. *Thomsonipollis magnificus* (Pflug & Thomson in Thomson & Pflug 1953) Krutzsch 1960.

Diagnosis. *Thomsonipollis* describes triporate pollen with complex pores and exine structure. The grain is circular to convex-triangular in polar view and oblate to spheroidal in equatorial view. The exine is composed of many layers, arranged into three lamella complexes without interlocula. The outer sculpture is pilate to scabrate. The pores are distinct, more or less equatorially arranged, and do not protrude beyond the equatorial margin. The exopore is large and slit-shaped to subcircular; the mesopore is formed by invagination of the middle layers of the exine (inner layers of the sexine and outer layers of the nexine in the type species), forming an endannulus that may show thickening; and the endopore is delineated by the inner layer of exine, and forms the atrium of the germinal apparatus. No other form genus has this combination of invaginated pores and complex laminated wall structure.

Elsik (1968b) broadened the generic diagnosis to accommodate his species *Thomsonipollis paleocenicus*, which was better suited to *Interpollis* and was transferred to that genus by Frederiksen (1980b). I therefore follow Srivastava (1972) and Tschudy (1975) in rejecting Elsik's (1968b) emendation of *Thomsonipollis*, as broadened the generic diagnosis to this extent greatly reduces its taxonomic utility, and brings it into conflict with *Interpollis*.

Thomsonipollis magnificus (Pflug & Thomson in Thomson & Pflug 1953) Krutzsch 1960
emend. Elsik 1968
Plate 5, figures 9-10

Intratropopollenites magnificus Pflug and Thomson in Thomson and Pflug, 1953, p. 88, pl. 9, fig. 112-124.

Thomsonipollis magnificus (Pflug & Thomson) Krutzsch, 1960, p. 58, 60, pl. 1, fig. 1-27; pl. 2, figs. 28-51; emend. Elsik, 1968b, p. 616, 618, pl. 20, fig. 3-17; pl. 21, fig. 1-6; Srivastava, 1972, p. 278, pl. 23, fig. 5-15; pl. 24, fig. 1-10; pl. 25, fig. 1-4; Tschudy, 1975, p. 24, pl. 14, fig. 13-20; Frederiksen, 1979, p. 153; Frederiksen, 1980a, p. 41, pl. 8, fig. 6; Harrington, 2003b, pl. 1, fig. 23; Jardine and Harrington, 2008, pl. 2, fig. 16.

Thomsonipollis magnificoides Krutzsch, 1960, p. 60, pl. 3, figs. 52-79, Text-Figure 3; Tschudy, 1975, p. 24, pl. 15, fig. 1-8.

Thomsonipollis spp. Tschudy, 1973a, p. B12, pl. 1, fig. 8-9.

Thomsonipollis aff. *T. magnificoides*. Tschudy, 1975, p. 24-25, pl. 15, fig. 9-20; Text-Figure 24.

Dimensions. Equatorial diameter 19 – 33 μm , mean 29 μm (10 specimens measured). Pflug and Thomson (in Thomson and Pflug, 1953) gave a range of 25 – 40 μm for the protologue specimens. Krutzsch (1960) gave a range of 25 – 50 μm , and Srivastava (1972) gave a range of 18 – 24 μm .

Remarks. This distinctive species is characterised by a thick wall with a complex internal structure, and a baculate to pilate surface sculpture. The pores are circular to elliptical, positioned equatorially to subequatorially, and are distinctly endannulate. A triangular area of thinner exine is sometimes present at one pole.

Although *Thomsonipollis magnificoides* differs from *Thomsonipollis magnificus* in having a thinner and more finely structured wall, previous workers (Elsik, 1968b; Srivastava, 1972; Tschudy, 1975; Frederiksen, 1979) have found that these species intergrade morphologically, and that intermediate forms are in practice hard to assign consistently to one or other species. I have therefore followed their precedent in counting all of these forms under *Thomsonipollis magnificus*.

Botanical affinity. Elsik (1968b) suggested Rubiaceae.

Occurrence. Occurred in relative abundances of <29% in 125/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. Occurrences above the lower part of the Claiborne Group on the Gulf Coast have been interpreted as reworked, but Frederiksen (1980a) reported perfectly preserved specimens from the Jackson and Vicksburg groups, potentially increasing the range of *Thompsonipollis* into the Early Oligocene.

“Thompsonipollis cf. T. expolita” of Frederiksen 1979

Plate 5, figure 11

Thompsonipollis magnificus (Pflug & Thomson in Thomson & Pflug 1953) Krutzsch 1960. Elsik, 1968b, p. 616, 618, pl. 20, fig. 6 – 7 only.

Thompsonipollis cf. T. expolitus Tschudy 1975. Frederiksen, 1979, p. 153, pl. 2, fig. 36 – 39; Harrington, 2003b, pl. 1, fig. 22.

Dimensions. Equatorial diameter 21 μm (one specimen measured). Tschudy (1975) gave a range of 16 – 24 μm for the *Thompsonipollis expolitus*. Frederiksen (1979) gave a range of 18 – 19 μm for *Thompsonipollis cf. T. expolita*.

Remarks. *Thompsonipollis expolita* Tschudy 1975 is distinguished by its round amb, smooth to weakly scabrate sculpture, exine clearly stratified into two equally thick layers, and circular pores marked by a pronounced invagination of the nexine, forming an endannulus. The nexine thins adjacent to the germinal. Frederiksen (1979) described specimens from the Late Paleocene of Virginia that were generally similar to *Thompsonipollis expolita*, but had a thinner, indistinctly stratified exine, and much less pronounced endannuli. Specimens recovered from my samples closely match the description given by Frederiksen (1979). Also similar are specimens illustrated by Elsik (1968b) from the Late Paleocene of Texas, which he identified as grains of *Thompsonipollis magnificus* in which the exine had been stripped off. Given the larger

size of most specimens of *Thompsonipollis magnificus*, and the limited stratigraphic occurrence of *Thomsonipollis* cf. *T. expolita* to the Late(est) Paleocene (see 'Occurrence', below), it seems more likely that this represents a separate taxon, distinct from *Thompsonipollis magnificus* and *Thompsonipollis expolita*. This latter species is apparently limited to the latest Maastrichtian on the US Gulf Coast (Tschudy, 1975).

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1% in 7/151 samples, in the Tuscahoma Formation on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Trivestibulopollenites* Pflug in Thomson & Pflug 1953

Type species. *Trivestibulopollenites betuloides* Pflug in Thomson and Pflug 1953.

Remarks. *Trivestibulopollenites* accommodates pollen with three vestibulate, equatorial pores. The amb is obtuse-convex-triangular, and the exine is smooth to granulate. The pores are positioned at the angles of the grain, and may be annulate or labrate. This genus differs from the Betulaceae/Myricaceae type in having vestibulate, and never atriate, pores. It differs from *Alnus* and *Alnipollenites* Potonié 1931 in consistently having three pores, and never displaying arci.

Trivestibulopollenites spp.

Plate 5, figure 12

Trivestibulopollenites spp. of the *T. betuloides* type. Tschudy, 1973a, p. B13, pl. 2, fig. 5-6.

Dimensions. Equatorial diameter 20 – 25 μm , mean 23 μm (five specimens)

measured).

Remarks. Specimens assigned to this taxon typically had prominent, annulate pores, with a narrow vestibulum. The exine is evenly granulate. As with the Betulaceae/Myricaceae type it proved difficult to consistently separate these specimens into form species, and so I have counted them as one taxon. Some specimens referred to *Trivestibulopollenites* spp. may correspond to *Trivestibulopollenites fissuratus* Frederiksen 1978.

Botanical affinity. Probably Betulaceae.

Occurrence. Occurred in relative abundances of <3.2% in 99/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Trudopollis* Pflug 1953 emend. Krutzsch in Góczán et al. 1967

Type species. *Trudopollis pertrudens* (Pflug in Thomson and Pflug 1953) Pflug 1953.

Remarks. *Trudopollis* is a form genus belonging to the Normapolle group, and is distinguished by a large vestibulum between the exopore and endopore, an interloculum between the sexine and nexine, and at least rudimentary oculi development. The amb shape is straight-triangular to convex-triangular or circular, and the grain is oblate in equatorial view. The sexine and nexine each comprise more than one layer, the outer surface is finely sculptured, and columellae may be present. The exopore is an equatorial lolate slit, and is typically annulate or tumescent. The inner layer of the sexine frequently shows structure adjacent to the germinal, such as radial bacula or punctae. The mesopore may be annulate or labrate. The endopore is atriate, with the atrium formed by the innermost layer of the nexine. There are no solution areas running over the poles.

Pompeckjoidaepollenites Krutzsch in Góczán et al. 1967 differs from *Trudopollis*

in having a solution channel over the poles, and in possessing circular or oval, rather than lolongate slit-shaped) exogerminals. *Oculopollis* and *Semioculopollis* Góczán et al. 1967 both show stronger oculi development and a different endopore structure to *Trudopollis*. *Basopollis*, *Choanopollenites*, *Complexiopollis* and *Nudopollis* do not possess oculi or interlocula, or have such a prominent vestibulum.

Trudopollis plenus Tschudy 1975

Plate 5, figure 13

Trudopollis pertrudens (Pflug in Thomson & Pflug 1953) Pflug 1953. Elsik, 1968b, p. 642 - 646, pl. 36, fig. 16; Fairchild and Elsik, 1969, p. 85, pl. 38, fig. 58-59.

Extratropopollenites nonperfectus Pflug in Thomson & Pflug 1953. Srivastava, 1972, p. 252, 254; pl. 13, fig. 5-11; pl. 14, fig. 1-4.

Trudopollis plenus Tschudy, 1975, p. 26, pl. 17, fig. 1-9; Text-Figure 27; Frederiksen, 1979, p. 155, pl. 3, fig. 11; Frederiksen, 1980b, p. 172, pl. 4, fig. 4-8.

Dimensions. Equatorial diameter 23 – 31 μm , mean 26, (six specimens measured).

Tschudy (1975) gave a range of 22 – 31 μm for the protologue specimens.

Remarks. This species is characterised by its relatively small annuli that only slightly protrude beyond the obtuse-straight- to obtuse-convex-triangular amb, a smooth to granulate surface ornamentation, mesopores that are larger than the exopores, and, in well-preserved specimens, a columellate interloculum. Weak plicae are sometimes present. The inner layer of the sexine is baculate at the germinals, and the vestibulum is very narrow. The endogerminal is atriate. Some of my specimens showed a slightly annulate or labrate mesogerminal, and are therefore similar to *Trudopollis* sp. A of Tschudy 1975. However, that taxon was limited to the Campanian, while in my material specimens with and without labrate mesogerminals co-occurred in the same samples, and the two forms appear to have a similar stratigraphic range. I have

therefore counted them together, thus allowing for some intra-specific variation in mesogerminal form within *Trudopollis plenus*. Frederiksen (1980b) emphasised the variability of this species, and documented coarsely verrucate grains from South Carolina (Frederiksen, 1980b, pl. 4, fig. 7). I only observed specimens with smooth or granulate surfaces in my samples.

Tschudy (1975) did not contrast *Trudopollis plenus* with other *Trudopollis* species, but it primarily differs in having less protruding annuli around the exopore, and in having a columellate interloculum. Other Gulf Coast species illustrated by Tschudy (1975) were more distinctly sculptured (verrucate or fossulate) and and/or had more prominent annuli.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <2% in 18/151 samples, from the Porters Creek to the Tuscaloosa formations on the eastern Gulf Coast.

“Trudopollis sp. B” of Tschudy 1975

Plate 5, figure 14

Trudopollis sp. B. Tschudy, 1975, p. 27-28, pl. 17, fig. 13-14; Text-Figure 30.

Dimensions. Equatorial diameter 26 µm. Tschudy (1975) gave a range of 25 – 29 µm for his specimens.

Remarks. Tschudy (1975) informally described this taxon based on four specimens from the Middle Paleocene of Louisiana. The amb is obtuse-straight- to obtuse-convex-triangular and the surface is granulate. The annulus is large, tear-shaped and structureless, and the vestibulum is prominent. The mesogerminal is slightly labrate, and there is a semi-circular notch below it. The specimen I have assigned to this taxon is very similar to Tschudy's (1975) illustrated grains. This taxon can be distinguished from *Trudopollis plenus* by its more prominent, tear-shaped annuli, and

by the semi-circular notch below the mesogerminal.

Botanical affinity. Unknown.

Occurrence. One specimen recorded, at the base of the Calvert Bluff Formation in Texas. This taxon has previously been recorded from the Naborton Formation of Louisiana (Tschudy, 1975), which is laterally equivalent to the Naheola Formation of Mississippi and Alabama (Fairchild and Elsik, 1969; Frederiksen and Warwick, 1995).

ZONOPORATE POLLEN

Genus *Alnus* Miller

Remarks. Pollen of extant *Alnus* possesses vestibulate, equatorial pores that are connected by arci on both faces of the grain. The pores are variable in number but there are typically between four and seven per grain; rarely there are just three. The pores may be labrate and occur at the angles of the grain, the amb of which will be triangular to heptagonal in shape depending on the number of pores. The exine is more or less smooth with some weak infratexture or surface sculpturing. Leaf fossils attributable to *Alnus* have been recovered from the Paleocene of North America (Wilson and Webster, 1946). The two species assigned to *Alnus* in this study possess morphological features that are characteristic of modern grains, and the use of the extant genus, rather than its associated form genus *Alnipollenites* Potonié 1931, is justified.

Trivestibulopollenites differs from *Alnus* in lacking arci, *Jarzenipollenites* Kedves 1980 possesses arci but lacks vestibula, and *Paraalnipollenites* lacks vestibula and shows false pores on its poorly developed arci. All three genera mainly comprise triporate forms. *Polyatriopollenites* is atriate and not vestibulate, and lacks arci. *Ulmipollenites* may possess arci, but the grains are verrucate to rugulate, and the pores are not vestibulate.

Alnus scotica Simpson 1961

Plate 5, figure 15

Alnus scotica Simpson 1961, p. 443, pl. 13, fig. 9-10.

Alnipollenites scoticus (Simpson) Pocknall and Nichols 1996, p. 32-33, pl. 7, fig. 15-16.

Dimensions. Equatorial diameter 26 – 28 μm (two specimens measured). Simpson (1961) gave a range of 35 – 45 μm for the protologue specimens.

Remarks. This taxon is distinguished from *Alnus verus* by the presence of a ring of thickened exine on one hemisphere. There are between five and seven pores, which are connected by arci. *Alnus bremanoirensis* Simpson 1961 differs in having a thicker polar ring and more elliptical pores. *Paraalnipollenites confusus* also has a ring of thickened exine on one hemisphere, but it lacks vestibula, is usually triporate, and often shows false pores on the arci.

Botanical affinity. *Alnus* (Betulaceae). Pocknall and Nichols (1996) listed several extant species of this genus that show a similar exinal ring.

Occurrence. Occurred in relative abundances of <1% in 10/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast.

Alnus verus (Potonié 1931) Martin & Rouse 1966

Plate 5, figures 16-17

Pollenites verus Potonié, 1931a, p. 332, pl. 2, fig. 40.

Alnipollenites verus (Potonié) Potonié, 1931b, p. 4, fig. 18.

Polyvestibulopollenites verus (Potonié) Thomson and Pflug, 1953, p. 90, pl. 10, fig. 62-76; Srivastava, 1972, p. 266, pl. 20, fig. 6.

Alnus verus (Potonié) Martin and Rouse, 1966, p. 196, fig. 69-71; Elsik, 1968b, p. 606-608, pl. 17, fig. 1-3; Frederiksen, 1980a, p. 42, pl. 8, fig. 9-10; Frederiksen, 1980b, p.

154-155; Frederiksen in Frederiksen et al., 1983, p. 43, pl. 13, fig. 2-3.

Dimensions. Equatorial diameter 23 – 31 μm , mean 26 μm (seven specimens measured). Potonié (1931b) gave a range of 17 – 21 μm for the protologue specimens. Thomson and Pflug (1953) gave a range of 18 – 35 μm for *Polyvestibulopollenites verus*, which is synonymous with *Alnus verus*.

Remarks. This is a generalised species of *Alnus*-like pollen, the major morphological features of which have been outlined in the genus remarks. *Alnus verus* lacks a polar ring of thickened exine, which differentiates it from *A. scotica*. Most of my specimens had five or six pores, but four and seven pored forms were also encountered.

Although Potonié's (1931b) original specimens were considerably smaller than my forms, and *Alnus speciipites* Wilson & Webster 1946 describes similar morphologies of this larger size, *Alnus verus* and its synonyms have had a much wider usage for *Alnus*-like pollen, regardless of grain size. I have therefore assigned my specimens to *Alnus verus* for the sake of consistency with the existing literature.

Botanical affinity. *Alnus* (Betulaceae).

Occurrence. Occurred in relative abundances of <15% in 49/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This species was much more common than *Alnus scotica* in my samples. It is known to range up into the Early Oligocene Vicksburg Group on the Gulf Coast.

Genus *Celtis* Linnaeus

Remarks. Pollen of extant *Celtis* is circular to polygonal in polar view, and has three to eight unevenly spaced pores located on or just off the equator. The pores are distinctly annulate and endannulate, and are more or less circular. The exine is

weakly columellate and smooth to scabrate to infragranulate (Frederiksen, 1980a). *Celtis* pollen therefore differs from other zonoporate pollen by its aperture structure (annulate and endannulate and not atriate or vestibulate), fine sculpture, and lack of arci.

Celtis tschudyi group of Frederiksen 1988

Plate 5, figure 18

Pollenites anulus (Potonié 1931) Potonié and Venitz 1934 [misidentified]. Engelhardt, 1964, p. 79, pl. 5, figs. 60-61.

Juglanspollenites sp. Tschudy and Van Loenen, 1970, pl. 3, figs. 29-30.

Multiporopollenites. spp. Tschudy, 1973a, p. B15, pl. 3, figs. 20-22.

Celtis tschudyi group (triporate) Frederiksen, 1988, p. 51, pl. 3, figs. 12-14.

Celtis tschudyi group (multiporate) Frederiksen, 1988, p. 51, pl. 3, figs. 15.

Celtispollenites sp. Harrington, 2003b, pl. 1, fig. 5.

Dimensions. Equatorial diameter 19 – 30 μm , mean 24 μm (six specimens measured). Elsik (1974b) gave a range of 22 – 37 μm for the protologue specimens of *Nothofagus tschudyi* (= *Celtis tschudyi* (Elsik 1974) Frederiksen 1980).

Remarks. This group comprises *Celtis tschudyi* (Elsik 1974) Frederiksen 1980, *Celtis texensis* Elsik 1974, and *Celtis sabinetownensis* (Elsik 1974) Frederiksen 1988. I have followed Frederiksen (1988) in counting these three species together because they intergrade to the extent that differentiating between them consistently is problematic. Additionally, Elsik (1974a, b) did not provide any differential diagnoses to distinguish between them. Specimens in my material have three to six \pm circular pores that 2 – 4 μm wide and are equatorially or slightly subequatorially arranged. Both the nexine and sexine thicken at the pores, forming both an annulus and an

endannulus, the endannulus being more prominent and distinct. The exine is finely infragranulate to scabrate, and weakly columellate. The amb is more or less circular. *Annutriparites rotundus* Frederiksen in Frederiksen et al 1983 is exclusively triporate, has a thinner exine, and is more distinctly columellate. *Myriophyllum* sp. is annulate but not endannulate, and has thicker exine that lacks columellae. *Nothofagus* pollen is colpoidate (Frederiksen, 1980a).

Botanical affinity. *Celtis* (Cannabaceae) (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <2.6% in 11/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast. This taxon is known to range up to the top of the Eocene on the US Gulf Coast (Frederiksen, 1988).

Genus *Juglans* Linnaeus

Remarks. Pollen of extant *Juglans* is typically polyporate-heteropolar, with 2 – 37 atriate pores. Morphological overlap with pollen of extant *Pterocarya* Nuttall ex Moquin-Tandon, which has 3 – 9 atriate pores and is typically zonoporate but may be polyporate-heteropolar as well, has led authors to assign *Juglans*-like fossil pollen to the form genus *Juglanspollenites* Raatz 1937 to reflect this uncertainty (Nichols, 1973; Wingate and Nichols, 2001). However, where the grain is polyporate-heteropolar and has over nine pores, as is the case with *Juglans nigripites*, the extant genus can justifiably be used (Nichols, 2010). *Juglans* pollen differs from that of *Celtis* by having atriate rather than endannulate pores, and by lacking columellae. *Polyatriopollenites* is exclusively zonoporate.

Juglans nigripites Wodehouse 1933

Plate 5, figure 21

Juglans nigripites Wodehouse, 1933, p. 504, fig. 31; Frederiksen, 1980b, p. 158, pl. 2, fig. 4-5; Frederiksen, 1980b, p. 43, pl. 8, fig. 16-17.

Juglans sp. Fairchild and Elsik, 1969, p. 84, pl. 37, fig. 14.

Multiporopollenites sp. Tschudy and Van Loenen, 1970, pl. 3, fig. 33.

Juglanspollenites nigripites (Wodehouse) Wingate and Nichols, 2001, p. 115.

Dimensions. Equatorial diameter 33 μm (one specimen measured). Specimens from Wodehouse's (1933) original material have a size range of 35 – 45 μm (Nichols, 2010).

Remarks. This species has eight \pm equatorial pores, and two or three pores situated near the pole on one hemisphere. The pores are annulate, and the exine is granulate. The amb is subcircular. This species differs from *Polyatriopollenites stellatus* by having a greater number of equatorial pores, and several pores located off the equator.

Botanical affinity. *Juglans* (Juglandaceae) (Nichols, 2010).

Occurrence. One specimen recorded from the Tallahatta Formation on the eastern Gulf Coast. This is the earliest recorded occurrence of this taxon the US Gulf Coast; it is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Genus *Malvacipollis* Harris 1965 emend. Krutzsch 1966

Type species. *Malvacipollis diversus* Harris 1965

Remarks. This genus includes finely echinate grains with circular amb. The spines may be evenly distributed or concentrated in groups near the pores. The pores are circular and may be annulate. *Compositoipollenites* differs in being more coarsely and densely echinate and in frequently showing a negative reticulum.

Malvacipollis spp.

Plate 5, figures 22-23

Echiperiporites spp. Tschudy, 1973a, p. B15, pl. 3, fig. 13-14.

Malvacipollis tschudyi (Frederiksen 1973) Frederiksen, 1980a, p. 44, pl. 8, fig. 27.

Malvacipollis sp. Frederiksen, 1980b, p. 156, pl. 1, fig. 32-38.

Malvacipollis spp. Pocknall and Nichols, 1996, p. 34, pl. 7, fig. 18-19.

Malvacipollis cf. *M. tschudyi*. Frederiksen, 1988, p. 52, pl. 5, fig. 10-14.

Dimensions. Greatest dimension (excluding spines) 22 – 29 μm , mean 24 μm (six specimens measured).

Remarks. Specimens assigned to *Malvacipollis* spp. are finely echinate with evenly distributed spines <2 μm high. The amb is circular, and the exine is distinctly columellate. The pores are endannulate and in a zonoporate orientation. Two specimens were recovered from the Late Paleocene Tuscahoma and Calvert Bluff formations; these are triporate and have an exine <1 μm thick. Specimens recovered from the Tallahatta Formation are much more abundant and generally have six or more pores and an exine 1 – 2 μm thick. Thus there seems to be two populations of *Malvacipollis* species in the Gulf Coast Palaeogene; one in the Late Paleocene that is rare and corresponds to *Malvacipollis* sp. of Frederiksen (1980b) and *Malvacipollis* spp. of Pocknall and Nichols (1996), and one in the Early to Middle Eocene that is common and corresponds to *Malvacipollis tschudyi* and *Malvacipollis* cf. *M. tschudyi* of Frederiksen (1988). More work needs to be carried out on the rare occurrences in the Early Eocene Hatchetigbee Formation to determine which population they belong too, and on the specimens in the Tallahatta Formation to determine whether both populations are present or just the more robust, multiporate form. *Malvacipollis spinulosa* Frederiksen in Frederiksen et al. 1983 is more finely spinate than the forms from the US Gulf Coast, has a thinner exine, and is larger (27 – 37 μm in diameter). **Botanical affinity.** Possibly Euphorbiaceae. The sexine is not thickened under the spines in my specimens, which suggests that Euphorbiaceae is a more likely affinity than Malvaceae (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <20% in 16/151 samples, from the Tuscaloosa to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. *Malvacipollis tschudyi* is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Genus *Myriophyllum* Linnaeus

Remarks. Pollen of extant *Myriophyllum* is tetraporate (rarely triporate or pentaporate), with annulate, slightly lalongate pores that are never vestibulate. The grains are suboblate and the exine is psilate to scabrate. The pores are typically asymmetrically distributed around the grain (i.e. more or less than 90° from each other). This suite of features is distinctive and unambiguous (Nichols, 2010), and so the use of the extant genus, rather than the associated form genus *Haloragacidites* Couper 1953, is permissible.

“*Myriophyllum* sp.” of Frederiksen 1980

Plate 5, figure 24

Myriophyllum sp. Frederiksen, 1980a, p. 42-43, pl. 8, figs. 13-14.

Dimensions. Equatorial diameter 25 µm. Frederiksen (1980a) gave dimensions of 25 x 28 µm for his specimen from the Late Eocene of Mississippi.

Remarks. This taxon is characterised by its oblate shape, psilate exine, and the presence of four distinctly annulate pores. The exine is 2 µm thick between the pores and 5 µm thick at the pores, forming annuli 8 – 10 µm wide. The ectopores are ~3 µm wide and circular to slightly lalongate. On my specimen the pores are not evenly positioned around the grain, and two are offset from the equator. In all other respects

the single grain in my material is a good match for that illustrated by Frederiksen (1980a). *Myriophyllum ambiguipites* Wodehouse 1933 has a thinner exine and less pronounced annuli.

Botanical affinity. *Myriophyllum* (Haloragaceae) (Frederiksen, 1980a).

Occurrence. One specimen recorded in the Zilpha Formation of the eastern Gulf Coast.

Genus *Polyatriopollenites* Pflug 1953

Type species. *Polyatriopollenites stellatus* (Potonié 1931) Pflug 1953.

Remarks. This form genus describes pollen that is similar to that of modern *Pterocarya* (Juglandaceae). It possesses between four and seven atriate pores, located equatorially or slightly subequatorially at the grain angles. The pores may be slightly annulate or labrate. The shape of the amb depends on the number of pores, and varies from quadrangular to heptagonal. The exine is finely but evenly granulate, and lacks columellae.

Polyatriopollenites stellatus (Potonié 1931) Pflug 1953

Plate 5, figure 25

Pollenites stellatus Potonié, 1931b, p. 4, fig. 20.

Polyatriopollenites stellatus (Potonié) Pflug 1953, p. 115, pl. 24, fig. 47; Frederiksen, 1979, p.154, pl. 3, fig. 9.

Pterocarya vermontensis Traverse, 1955, p. 45, fig. 9(29).

Polyatriopollenites vermontensis (Traverse) Frederiksen, 1980b, p. 157-158; Frederiksen in Frederiksen et al., 1983, p. 43, pl. 13, fig. 4-5; Pocknall and Nichols, 1996, p. 34-35, pl. 7, fig. 20-21.

Pterocarya sp. Elsik, 1968b, p. 606, pl. 16, fig. 25.

Pterocarya stellatus (Potonié) Martin and Rouse 1966. Frederiksen, 1980a, p. 43, pl. 8, fig. 15.

Dimensions. Equatorial diameter 29 – 33 μm (two specimens measured). Potonié (1931b) gave a size of 38 μm for *Pollenites stellatus*; Traverse (1955) gave a size of ~37 μm for *Pterocarya vermontensis*.

Remarks. The major distinguishing features of this taxon have been described in the genus remarks. My specimens all had five or six atriate pores that lay on or very near to the equator. A slight annular thickening or labrum was present on most specimens. The sides of the amb between the pores were more or less straight. *Polyatriopollenites stellatus* is similar to *Juglanspollenites nigripites* in terms of aperture style, but this latter taxon differs in having a greater number of pores, some of which are located near one pole.

Frederiksen (1980b) argued that species of *Polyatriopollenites* could be distinguished based on the height of the labra, and suggested that North American forms, having generally lower labra than European types, should be assigned to *Polyatriopollenites vermontensis* rather than *Polyatriopollenites stellatus*. However, given the variable nature of the labra in these taxa (Frederiksen, 1980b), consistently assigning specimens to species based on this criterion seems problematic, and species distinctions based solely on geographic range is undesirable. I have therefore treated *Polyatriopollenites stellatus* and *Polyatriopollenites vermontensis* as being synonymous.

Botanical affinity. Juglandaceae; probably *Pterocarya* (Pocknall and Nichols, 1996). There is a degree of morphological continuity between pollen of modern *Pterocarya* and *Juglans*, which makes this suggested affinity uncertain (Nichols, 1973). However, macrofossils of *Pterocarya* are widespread in the Palaeogene deposits of North America (see references in Frederiksen, 1980b, p. 157), suggesting that at least some of the specimens assigned to *Polyatriopollenites stellatus* were produced by this genus.

Occurrence. Occurred in relative abundances of <4% in 59/151 samples, from the

Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. In the south eastern US this species is thought to range into the Miocene or Pliocene (Frederiksen, 1980b).

Genus *Ulmipollenites* (Wolff 1934) Srivastava 1969

Type species. *Ulmipollenites undulosus* Wolff 1934.

Remarks. *Ulmipollenites* includes zonoporate pollen with a verrucose to rugulate exine. Arci are frequently present in this genus, but are often only weakly expressed. The pores are distinctly annulate. Species assigned to *Alnus* differ in having a granulate exine, vestibulate pores, and consistently distinct arc; those assigned to *Polyatriopollenites* differ in having a granulate exine and lacking arc.

Ulmipollenites krempii (Anderson 1960) Frederiksen 1979

Plate 5, figures 26-27

Ulmoideipites krempii Anderson, 1960, p. 20, pl. 4, fig. 12; pl. 6, figs. 2-3; pl. 10, fig. 8; Elsik, 1968b, p. 608, pl. 17, fig. 4-7; Srivastava, 1972, p. 280, pl. 25, fig. 19; Jaramillo and Dilcher, 2001, p. 171-172, pl. 21, fig. 27.

Ulmipollenites krempii (Anderson) Frederiksen, 1979, p. 154, pl. 3, fig. 6-8; Frederiksen, 1980b, p. 156, pl. 1, fig. 39-40; Frederiksen in Frederiksen et al., 1983, p. 35, pl. 9, fig. 9-10, Pocknall and Nichols, 1996, p. 35-36, pl. 7, fig. 22; Jardine and Harrington, 2008, pl. 2, fig. 18.

Dimensions. Equatorial diameter 23 – 29 μm , mean 26 μm (six specimens measured). Anderson (1960) gave a range of 16 – 26 μm for the protologue specimens.

Remarks. This species includes specimens with three or more annulate pores, a

verrucate sculpture, and arci connecting the pores. The sides of the amb are convex. My specimens had between three and five pores, and the arci, if present, were weakly expressed. The development of the verrucae was also variable among specimens.

Ulmipollenites tricostatus is consistently triporate and has more distinct arci, and *Ulmipollenites undulosus* is rugulate.

Botanical affinity. Ulmaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <4% in 44/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. *Ulmipollenites krempii* was much more common than the two other *Ulmipollenites* species in this study.

Ulmipollenites tricostatus (Anderson 1960) Frederiksen 1980

Plate 5, figure 28

Ulmoidipites tricostatus Anderson, 1960, p. 20-21, pl. 4, fig. 9-11; pl. 6, fig. 4-5; pl. 7, fig. 8; pl. 8, fig. 8-9.

Ulmipollenites tricostatus (Anderson) Frederiksen, 1980b, p. 156-157, pl. 1, fig. 41; Frederiksen in Frederiksen et al., 1983, p. 35, pl. 9, fig. 11-13; Pocknall & Nichols, 1996, p. 36, pl. 7, fig. 23.

Dimensions. Equatorial diameter 24 μm (one specimen measured). Anderson (1960) gave a range of 17 – 23 μm for the protologue specimens.

Remarks. This taxon is triporate and has straight to slightly convex sides and distinct arci. Like *Ulmipollenites krempii* the exine is verrucate, but the amb shape, number of pores and the nature of the arci differentiate these two species. *Ulmipollenites undulosus* differs in being rugulate. This species also has a general resemblance to *Momipites* cf. *M. flexus*, but differs in being verrucate as opposed to evenly granulate.

Botanical affinity. Ulmaceae (Pocknall and Nichols, 1996).

Occurrence. Two specimens observed in the Hatchetigbee Formation of the eastern Gulf Coast.

Ulmipollenites undulosus Wolff 1934

Plate 5, figure 29

Ulmipollenites undulosus Wolff, 1934, p. 75, pl. 5, fig. 25; Frederiksen, 1980b, p. 157, pl. 2, fig. 1-3; Frederiksen in Frederiksen et al., 1983, p. 35, pl. 9, fig. 14-15.

Dimensions. Equatorial diameter 30 μm (one specimen measured). Wolff (1934) gave a size of 35 μm for the holotype.

Remarks. This taxon has distinctly convex sides and a rugulate exine. Arci, if present, are indistinct. My specimens had four or five pores. *Ulmipollenites undulosus* differs from the other *Ulmipollenites* species in this study by having a rugulate, rather than verrucate exine.

Botanical affinity. Ulmaceae (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <1.1% in 3/151 samples, in the Hatchetigbee Formation on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This species is known to range into the Late Oligocene in the south eastern United States (Frederiksen, 1980b).

PERIPORATE POLLEN

Genus *Chenopodipollis* Krutzsch 1966

Type species. *Chenopodipollis multiplex* (Weyland and Pflug 1957) Krutzsch 1966.

Remarks. This genus includes periporate pollen with a punctate, columellate exine. It differs to *Periporopollenites* Pflug & Thomson in Thomson & Plug 1953 by having a

punctate, rather than granulate exine, and more distinct columellae.

Chenopodipollis spp.

Plate 5, figure 30

Chenopodiaceae. Elsik, 1968a, pl. 15, fig. 9-12; Elsik, 1968b, p. 599.

Chenopodipollis sp. Frederiksen, 1980b, p.158, pl. 2, fig. 6.

Dimensions. Greatest dimension 26 – 28 μm (two specimens measured).

Remarks. My specimens of *Chenopodipollis* are distinctly punctate and columellate, and have approximately 30 – 40 circular pores evenly distributed over the grain surface. Pocknall and Nichols (1996) recovered superficially similar forms from the Late Paleocene of the Western Interior, but which were granulate rather than punctate and so properly assigned by Pocknall and Nichols (1996) to *Periporopollenites*.

Botanical affinity. Possibly Chenopodiaceae or Amaranthaceae (Frederiksen, 1980b).

Occurrence. Occurred in relative abundances of <3% in 22/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Erdtmanipollis* Krutzsch 1962

Type species. *Erdtmanipollis pachysandroides* Krutzsch 1962.

Remarks. This distinctive genus is distinguished by its crotonoid-reticulate sexine, which does not have a covering reticulum. The nexine is smooth and structureless. The pores are distributed evenly across the grain, with each occurring in the middle of a lumen. *Thymelipollis* Krutzsch 1966 differs in possessing a thicker exine that is

surficially crotonoid but has a more complex internal structure.

Erdtmanipollis cretaceus (Stanley 1965) Norton in Norton & Hall 1969

Plate 6, figures 1-2

Pachysandra cretaceus Stanley 1965, p. 294, pl. 44, figs. 1-9.

Erdtmanipollis cretaceus (Stanley) Norton in Norton and Hall 1969, p. 43, pl. 5, fig. 21;

Pocknall and Nichols 1996, p. 36-37, pl. 7, fig 26-27.

Dimensions. Greatest dimension 26 – 36 μm (two specimens measured). Stanley (1965) gave a range of 20 – 40 μm for the protologue specimens.

Remarks. *Erdtmanipollis cretaceus* includes spheroidal grains with a crotonoid-reticulate sculpture. The pores are small and indistinct, and number about 30 across the grain. *Erdtmanipollis pachysandroides* Krutzsch 1962 and *Erdtmanipollis procombentiformis* (Samoilovich 1961) Krutzsch 1962 differ in having a more open reticulate sculpture, and in being larger.

Botanical affinity. Buxaceae. Pocknall and Nichols (1996) likened this species to pollen of the modern genera *Pachysandra* and *Sarcococca*, which currently occur in southeastern North America.

Occurrence. Four specimens recorded from the Porters Creek and Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Periporate genus A

Plate 6, figures 3-4

Thymelaeaceae (?). Elsik, 1968a, pl. 15, fig. 14; Elsik, 1968b, p. 600.

Description of current specimens. Monad pollen, radial, isopolar, grain \pm spheroidal; periporate, pores annulate, 2 μm in diameter, ~ 20 in number, distributed evenly over the grain surface; exine 1.5 – 2 μm thick, sexine:nexine ratio $\sim 2:1$, sexine columellate, semi-ectate, muri-clavate reticulate, heterobrochate, lumina 0.5 – 1 μm wide, muri ~ 0.3 μm wide.

Dimensions. Equatorial diameter 26 – 29 μm (two specimens measured).

Remarks. This taxon is characterised by its reticulate sculpture and spheroidal shape. Of the most similar periporate form genera, *Thymelipollis* Krutzsch 1966 has a thicker exine that is superficially crotonoid and has a more complex internal structure, and *Buxapollis* Krutzsch 1966, although microreticulate, has a greater number of pores that are < 1 μm in diameter and not annulate. *Chenopodipollis* has a minutely punctate exine.

Botanical affinity. Elsik (1968b) tentatively referred this taxon to Thymelaeaceae. The majority of genera within this family have a crotonoid-reticulate sculpture, whereas this taxon is microreticulate. *Daphne* however, does have a reticulate sexine, as do various genera of the Buxaceae (Erdtman, 1952).

Occurrence. Two specimens recorded from the Calvert Bluff Formation of Texas.

Genus *Wodehouseia* Stanley 1961

Type species. *Wodehouseia spinata* Stanley 1961.

Remarks. This genus includes tetraporate pollen that has two elliptical pores on each hemisphere. The grain is oblate in shape and the amb is elliptical; each pore is positioned $\sim 1/4$ the way along the long axis of the ellipse. An equatorial cingulum-like flange, reinforced with spines, is always present in this genus. The exine is granulate and further ornamented with sparsely distributed spines.

Wodehouseia spinata Stanley 1961

Plate 6, figure 5

Wodehouseia spinata Stanley, 1961, p. 157, pl. 1, fig. 1-3.

Dimensions. Length 33 μm ; width 17 μm (excluding flange; one specimen measured). Stanley (1961) gave a range of 35 – 50 μm x 15 – 25 μm for the protologue specimens.

Remarks. The major morphological features of this species have been detailed in the genus remarks. The flange is punctate in plan view, and on my specimen it is 8 μm wide at the middle of the lateral edges of the grain, and 3 μm wide at the grain ends.

Botanical affinity. Unknown.

Occurrence. One specimen recorded in the Nanafalia Formation on the eastern Gulf Coast. This species is more common in Late Cretaceous sediments, and is probably reworked (Fairchild and Elsik, 1969).

MONOSULCATE POLLEN

Genus *Arecipites* Wodehouse 1933 emend. Nichols et al 1973

Type species. *Arecipites punctatus* Wodehouse 1933.

Remarks. *Arecipites* includes tectate pollen grains with a psilate to punctate sculpture, and a sulcus that is tapered at the ends. *Liliacidites* differs in being reticulate and semi-tectate, and *Monocolpopollenites* differs in having a colpus that has flared or rounded ends.

Arecipites spp.

Plate 6, figures 6-7

Arecipites sp. Jardine and Harrington, 2008, pl. 2, fig. 20.

Dimensions. Length 29 μm , width 21 μm (one specimen measured).

Remarks. Specimens referable to *Arecipites* were widespread but not abundant in my samples. Subtle variations in exine thickness, sculpture and overall size made subdividing these grains into species difficult, and I counted them together as one taxon.

Botanical affinity. Probably Arecaceae (Nichols et al., 1973).

Occurrence. Occurred in relative abundances of <3.2% in 91/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Cycadopites* Wodehouse 1933 ex Wilson & Webster 1946

Type species. *Cycadopites follicularis* Wilson & Webster 1946.

Remarks. *Cycadopites* pollen has an ellipsoidal amb that is about twice as long as wide, and one long sulcus that extends the full length of the grain. The sulcus is constricted and often closed in the middle, and gapes open at either end. The exine is smooth or very finely textured. Pollen of *Monocolpopollenites* is smaller, and has a shorter colpus that is not closed in the middle.

Cycadopites follicularis Wilson & Webster 1946

Plate 6, figure 8

Cycadopites follicularis Wilson and Webster, 1946, p. 274-275, fig. 7; Jardine and Harrington, 2008, pl. 1, fig. 14.

Dimensions. Length 37 – 59 μm , width 21 – 28 μm (two specimens measured).

Wilson and Webster (1946) gave a length of 39 – 42 μm and a width of 18 – 21 μm for the protologue specimens.

Remarks. The exine of this species is smooth. My specimens are larger than those of Wilson and Webster (1946) but are otherwise in good agreement with their description. *Cycadopites giganteus* Stanley 1965 is larger still (50 – 72 μm long). *Cycadopites scabratus* Stanley 1965 is smaller (30 – 34 μm long) and has a scabrate sculpture.

Botanical affinity. Cycadaceae (Wilson and Webster, 1946).

Occurrence. Occurred in relative abundances of <7% in 118/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Liliacidites* Couper 1953

Type species. *Liliacidites kaitangataensis* Couper 1953.

Remarks. As with *Arecipites* pollen of *Liliacidites* has a sulcus with tapered ends. *Liliacidites* differs from *Arecipites* in being coarsely muri-clavate reticulate rather than punctate to psilate (Nichols et al., 1973). The reticulum on the type species of *Liliacidites* fines from the central part of the grain to the ends, but this is not characteristic of the genus under Couper's (1953) original diagnosis.

Liliacidites spp.

Plate 6, figures 9-11

Liliacidites sp. Jardine and Harrington, 2008, pl. 2, fig. 22.

Dimensions. Length 31 – 44 μm , mean 37 μm ; width 23 – 29 μm , mean 27 μm (five specimens measured).

Remarks. *Liliacidites* pollen varied considerably in the coarseness of the reticulation and the size and shape of the grain. It was challenging, and not obviously advantageous, to assign these forms to species level, and I have counted them together at genus level. Some grains (e.g. Plate 6, figure 10) may represent *Liliacidites vittatus* Frederiksen 1973, extending its range down into the Late Paleocene.

Botanical affinity. Probably Arecaceae, but other monocot families such as Liliaceae, Amaryllidaceae, and Iridaceae may have been producers of these pollen types (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <5.5% in 73/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Longapertites* van Hoeken-Klinkenburg 1964

Type species. *Longapertites marginatus* van Hoeken-Klinkenburg 1964.

Remarks. *Longapertites* comprises monosulcate pollen with an arched distal side and a flat or slightly convex proximal side. The sulcus extends the whole length of the distal side, and is thus more than half as long as the grain circumference. Both *Cycadopites* and *Matanomadhiasulcites* have long sulci, but on these genera the sulcus is not longer than half the circumference of the grain and is limited to one hemisphere. *Proxapertites* and *Spinizonocolpites* are zona-sulcate rather than longisulcate. According to Zetter et al. (2001) some records of *Longapertites* are misidentifications of individual halves of *Proxapertites* that have become folded.

Longapertites spp.

Plate 6, figures 12-13

Dimensions. Length 31 – 59 μm , mean 44 μm ; width 19 – 31 μm , mean 25 μm (seven specimens measured).

Remarks. Specimens I have assigned to *Longapertites* spp. correspond well with those illustrated by Frederiksen (1988, 1998) from the Late Paleocene and Eocene of the US Gulf Coast. The exine is finely punctate to micro-reticulate, and is 0.75 – 1.5 μm thick. The distal side of the grain ranged from arched to angular. It was not possible to consistently assign these forms to species level, and I have followed Frederiksen (1988, 1998) in combining them into one generalised group.

Botanical affinity. Frederiksen (in Frederiksen et al., 1983) suggested Arecaceae, Liliaceae, Commelinaceae, Araceae, or Asparagaceae. Jaramillo et al. (2010) assigned all forms of *Longapertites* to Annonaceae.

Occurrence. Occurred in relative abundances of <3.1% in 45/151 samples, from the Nanafalia to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Matanomadhiasulcites* Kar 1985

Type species. *Matanomadhiasulcites maximus* (Saxena 1979) Kar 1985.

Remarks. This genus describes very large reticulate to foveolate pollen grains that are oval to elliptical in polar view, and possess a long and frequently gaping single sulcus. *Proxapertites* differs in being zona-colpate; *Longapertites* differs in having a sulcus that is longer than half the of the grain circumference. *Liliacidites* differs in being smaller and in having a sulcus that does not gape open.

Matanomadhiasulcites maximus (Saxena 1979) Kar 1985

Plate 6, figures 14-15

Matanomadhiasulcites maximus (Saxena 1979) Kar 1985; Frederiksen, 1994a, pl. 5, fig. 8

– 9; pl. 6, fig. 1-3; Frederiksen, 1998, pl. 2, fig. 12 – 13.

Dimensions. Length 81 – 148 μm , mean 132 μm (three specimens measured); width 98 – 108 (two specimens measured). Frederiksen (1998) gave length measurements of 133 μm and 153 μm for two grains from the Tusahoma Formation of Mississippi.

Remarks. The major features of this species have been described in the genus remarks. The exine is foveolate and the columellae are thick. Grains of *Proxapertites* in my material were either psilate or coarsely reticulate, and never foveolate.

Botanical affinity. Possibly Annonaceae (Frederiksen, 1998).

Occurrence. Occurred in relative abundances of <1.3% in 17/151 samples, from the Nanafalia to the Tallahatta formations on the eastern Gulf Coast. *Matanomadhiasulcus maximus* ranges down to at least the Naheola Formation on the US Gulf Coast (Frederiksen, 1998).

Genus *Monocolpopollenites* Pflug & Thomson in Thomson & Pflug 1953 emend.

Nichols et al. 1973

Type species. *Monocolpopollenites tranquillus* (Potonié 1934) Thomson & Pflug 1953.

Remarks. This genus includes pollen with one sulcus that has flared or rounded, and never tapered or open, ends. The amb is oval. The exine is psilate, scabrate or reticulate, but not granulate or verrucate. It differs from *Arecipites*, *Cycadopites* and *Liliacidites* by the morphology of the sulcus.

Monocolpopollenites tranquillus (Potonié 1934) Thomson & Pflug 1953

Plate 6, figure 16

Pollenites tranquillus Potonié, 1934, p. 51, pl. 2, fig. 3, 8.

Monocolpopollenites tranquillus (Potonié) Thomson and Pflug, 1953, p. 62-63, pl. 4, fig. 24-37, 39-47; Frederiksen, 1980a, p. 45, pl. 9, fig. 5; Jardine and Harrington, 2008, pl. 2, fig. 23.

Dimensions. Length 22 – 28 μm , mean 25 μm ; width 16 – 22 μm , mean 20 μm (five specimens measured). Potonié (1934) gave a length of about 24 μm for the protologue specimens.

Remarks. This species of *Monocolpopollenites* has a weakly granulate exine and is indistinctly tectate. The sulcus extends over $\frac{3}{4}$ the length of the grain.

Botanical affinity. Possibly Arecaceae (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <2% in 47/151 samples, from the Porters Creek to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Genus *Proxapertites* van der Hammen 1956 emend. Singh 1975

Type species. *Proxapertites operculatus* (van der Hammen 1954) van der Hammen 1956

Remarks. *Proxapertites* includes circular to subcircular zona-sulcate pollen. The grain often splits and appears as two separate halves in preparations. The exine ornamentation is variable among species. Specimens recovered from the Gulf Coast are either psilate to faintly punctate, or coarsely reticulate. Frederiksen (1988) assigned Gulf Coast *Proxapertites* types to one generalised taxon, but I have split my specimens into two informal groups based on exine ornamentation. *Proxapertites* from the US Gulf Coast requires further study, to properly link these forms with occurrences in South America, Asia, Africa and Europe. *Spinizonocolpites* is also zona-

sulcate but possesses supratectal spines. *Matanomadhiasulcites* and *Longapertites* are longiscutate rather than zona-sulcate.

Proxapertites (psilate type)

Plate 6, figure 17

Proxapertites sp. Frederiksen, 1998, pl. 2, fig. 7 – 8.

Proxapertites psilatus Sarmiento 1992. Harrington, 2003b, pl. 1, fig. 16.

Dimensions. Length 34 – 59 μm , mean 44 μm ; width 21 – 47 μm , mean 34 μm (seven specimens measured).

Remarks. This taxon includes psilate to weakly punctate zona-sulcate pollen. The exine is 0.5 – 1 μm thick. The grain usually appears with both halves still attached to one another, although isolated halves were observed. This taxon may be conspecific with *Proxapertites psilatus* Sarmiento 1992.

Botanical affinity. Probably Araceae (Frederiksen, 1998).

Occurrence. Occurred in relative abundances of <4% in 65/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Proxapertites (reticulate type)

Plate 6, figure 18

Proxapertites spp. Tschudy, 1973a, pl. 3, fig. 1 – 4.

Proxapertites spp. Frederiksen, 1988, pl. 6, fig. 3 – 11.

Dimensions. Length 36 – 43 μm ; width 30 – 34 μm (two specimens measured).

Remarks. This taxon includes coarsely reticulate zona-sulcate pollen. My specimens

exhibited all of the morphological variability shown by the illustrated specimens in Frederiksen (1988) and Tschudy (1973a). The exine is up to 3 μm thick and coarsely muri-clavate, the lumina are typically 1 – 2 μm wide, and the muri are 0.5 – 1 μm wide and simpli- to duplibaculate. The grain is almost always entire. Some of these specimens probably represent *Proxapertites cursus* Van Hoeken-Klinkenberg 1966; others may represent *Proxapertites emendatus*.

Botanical affinity. Probably Araceae (Jaramillo et al., 2010)

Occurrence. Occurred in relative abundances of <3% in 9/151 samples, from the Hatchetigbee and Tallahatta formations on the eastern Gulf Coast.

Genus *Spinizonocolpites* Muller 1968 emend. Muller et al. 1987

Type species. *Spinizonocolpites echinatus* Muller 1968.

Remarks. *Spinizonocolpites* accommodates pollen of the type produced by the extant palm *Nypa*. The pollen grain is zona-colpate, and has a smooth, punctate or microreticulate exine that is covered with sparsely distributed supratectal baculae or echinae. *Proxapertites* differs in not possessing supratectal spines, and *Mauritiidites* Van Hoeken-Klinkenburg 1964 differs in being mono- rather than zona-colpate, and in having spines that project from the exine base, with the sexine indented around them.

Spinizonocolpites prominatus (McIntyre 1965) Stover & Evans 1973

Plate 6, figure 19

Spinizonocolpites prominatus (McIntyre 1965) Stover & Evans 1973. Frederiksen, 1994a, p. 118, 120, pl. 10, fig. 1-9.

Spinizonocolpites echinatus Muller, 1968, p. 11-12, pl. 3, fig. 3.

Nypa echinata (Muller) Frederiksen, 1980a, p. 46, pl. 9, fig. 18-21.

Dimensions. Length 38 μm , width 23 μm (one specimen measured; both dimensions excluding spines).

Remarks. *Spinizonocolpites prominatus* has conical spines 4 – 9 μm long. The exine is microreticulate and columellate. *Spinizonocolpites baculatus* Muller 1968 has baculate, rather than conical, elements that are longer, at 7 – 13 μm long; *Spinizonocolpites adamanteus* Frederiksen 1994 has elements that are rounded-diamond shaped in side view; *Spinizonocolpites grandis* Jaramillo & Dilcher 2001 is larger (length 70 – 85 μm).

Botanical affinity. *Nypa* (Arecaceae) (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <2% in 8/151 samples, from the Tuscaloosa to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This Taxon is known to range up into the Late Eocene Yazoo Clay on the eastern Gulf Coast (Frederiksen, 1980a).

DICOLPATE POLLEN

Genus *Dicolpopollis* Pflanzl 1956 ex Potonié 1966

Type species. *Dicolpopollis kockelii* Pflanzl 1956 ex Potonié 1966.

Remarks. This genus includes dicolpate pollen with a microreticulate, granulate or microverrucate exine. *Disulcites* Erdtman 195 ex Potonié 1966 differs in having two sulci rather than two colpi (i.e. two furrows that run latitudinally rather than longitudinally). *Disulcipollis* Krutzsch 1970 differs in being smooth to finely punctate but not reticulate.

Dicolpopollis spp.

Plate 6, figure 20

Dicolpopollis cf. *D. kalewensis* Potonié 1960. Tschudy, 1973a, p. B14, pl. 2, fig. 27-29.

Dicolpopollis spp. Frederiksen, 1988, pl. 6, fig. 12 – 19.

Dimensions. Length 24 µm, width 20 µm (one specimen measured).

Remarks. Pollen of this type is dicolpate with a microreticulate exine. The colpi are gaping and extend about $\frac{3}{4}$ of the way to the pole. The lumina are ~0.5 µm near the pole, and fine to <0.25 µm near the colpi margins and equator. These specimens match closely with those illustrated by Tschudy (1973a) and Frederiksen (1988).

Botanical affinity. Tschudy (1973a) suggested Amaryllidaceae, Arecaceae or Cunoniaceae as possible parent plant families.

Occurrence. Occurred in relative abundances of <1.2% in 3/151 samples, in the Hatchetigbee Formation on the eastern Gulf Coast. This taxon has also been recorded from the Reklaw Formation of Texas (Tschudy, 1973a), which is laterally equivalent to the Tallahatta Formation on the eastern Gulf Coast.

TRICOLPATE POLLEN

Genus *Acer* Linnaeus

Remarks. Pollen of modern *Acer* is tricolpate to tricolporoidate, with long, wide colpi and a reticulate to faintly striate exine. The most appropriate form genus for this type of pollen is *Aceripollenites* Nagy 1969. *Striatopollis* is fully striate.

Acer? striatellum (Takahashi 1961) Frederiksen 1980

Plate 7, figure 1

Tricolpopollenites striatellus Takahashi, 1961, p. 319, pl. 23, fig. 50-51

Acer? striatellum (Takahashi) Frederiksen, 1980a, p. 50, pl. 11, fig. 4-5.

Dimensions. Polar diameter 40 µm; equatorial diameter 25 µm (one specimen measured).

Remarks. This species is distinguished by its prolate shape, gaping colpi and a muri-clavate reticulate exine that is locally striate. *Striatopollis terasmaei* (Rouse 1962) Frederiksen 1980 differs in having geniculate colpi and a more variable shape.

Botanical affinity. Probably *Acer* (Sapindaceae) (Frederiksen, 1980a).

Occurrence. One specimen recorded, in the Hatchetigbee Formation on the US Gulf Coast. This species is known to range up into the Early Oligocene Vicksburg Group. (Frederiksen, 1980a).

Genus *Cupuliferoideaepollenites* Potonié et al 1950 ex. Potonié 1960

Type species. *Cupuliferoideaepollenites liblarensis* (Thomson in Potonié et al 1950) Potonié 1960.

Remarks. This genus includes tricolpate, prolate pollen with well-rounded poles. The exine is psilate and not columellate, although there may be a faint infratexture. *Cupuliferoipollenites* is similar but accommodates tricolporate rather than tricolpate pollen.

Cupuliferoideaepollenites spp.

Plate 7, figures 2-3

Tricolpopollenites liblarensis (Thomson in Potonié et al. 1950) Thomson & Pflug 1953. Tschudy, 1973a, p. B18, pl. 4, fig. 31-33.

Cupuliferoideaepollenites liblarensis (Thomson) Potonié 1960. Frederiksen, 1980a, p. 47, pl. 9, fig. 23.

Cupuliferoideaepollenites spp. Frederiksen, 1980b, p. 161; Frederiksen in Frederiksen et

al., 1983, p. 50, pl. 14, fig. 20-21.

Dimensions. Polar diameter 15 – 19 μm , mean 18 μm ; equatorial diameter 9 – 18 μm , mean 15 μm (three specimens measured).

Remarks. *Cupuliferoidaepollenites* spp. includes small prolate to spherical grains with a psilate exine that is not columellate. I have followed Frederiksen (1980b) in grouping all specimens of this general type together, due to the difficulties of consistently separating them into species. This taxon differs from *Eucommia* spp. in being consistently smaller and never colpor(oid)ate.

Botanical affinity. Frederiksen (1980a) suggested Fagaceae or possibly Fabaceae as likely parent families.

Occurrence. Occurred in relative abundances of <1.9% in 7/151 samples, from the Tuscaloosa to the Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group on the Gulf Coast (Frederiksen, 1980a).

Genus *Eucommia* Oliver

Remarks. Pollen of modern *Eucommia* is tricolpate to weakly tricolporate, has a psilate to weakly scabrate exine, and has colpi bordered by narrow thickened margins. The colpi are not always of the same length (Erdtman, 1952). Leaves, fruits and inflorescences attributable to *Eucommia* have been recorded from the Early Eocene of North America (Call and Dilcher 1997) *Cupuliferoidaepollenites* types differ in being smaller and exclusively tricolpate.

Eucommia spp.

Plate 7, figures 4-5

Eucommia? leopoldae Frederiksen in Frederiksen et al., 1983, p. 59-60, pl. 17, figs. 7-13;
Pocknall and Nichols, 1996, p. 19-20, pl. 4, figs. 27-30.

Eucommia sp. 1. Jardine and Harrington, 2008, p. 195, pl. 2, fig. 24.

Dimensions. Polar diameter 26 – 34 μm , mean 31 μm ; equatorial diameter 21 – 27 μm , mean 24 μm (eight specimens measured). Frederiksen (in Frederiksen et al 1983) gave a range of 27 – 29 μm for the polar diameter of *Eucommia? leopoldae*; Pocknall and Nichols (1996) gave a range of 22 – 30 μm for the polar diameter and 16 – 24 μm for the equatorial diameter for the same taxon.

Remarks. I have grouped together all *Eucommia*-type pollen into one generalised group, which includes tricolpate to tricolpor(oid)ate forms. Although it would be possible to count forms with and without pores separately (e.g. Frederiksen, 1988), in practice I found it problematic to consistently distinguish between colpate and incipiently colporate forms, and the specimens in my material appear to belong to a morphological continuum with truly colpate and colporate end-members. Colpate forms were rare compared to colpor(oid)ate, and given the similar stratigraphic range of these forms there is little benefit in splitting them further. Pocknall and Nichols (1996) broadened the circumscription of *Eucommia? leopoldae* Frederiksen in Frederiksen et al 1983 to include incipiently tricolporate forms as well as the distinctly tricolpate forms described and illustrated by Frederiksen (in Frederiksen et al 1983). My specimens therefore include this taxon as well as tricolpate *Eucommia* types.

In all other respects the specimens in my material match well with previously illustrated *Eucommia* pollen from North America. The grains are subprolate with straight to slightly convex sides and are flattened at the poles. The exine is psilate to scabrate and internally structureless. The colpi are bordered by narrow thickenings and are $\sim 2/3$ the length of the grain, but may be artificially extended by exinal folds.

Botanical affinity. *Eucommia* (Eucommiaceae) (Frederiksen in Frederiksen et al.,

1983).

Occurrence. Occurred in relative abundances of <3% in 35/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation of Texas.

Genus *Insulapollenites* Leffingwell 1971

Type species. *Insulapollenites rugulatus* Leffingwell 1971.

Remarks. This form genus includes oblate, parasyncolpate pollen with both polar and equatorial islands, which are formed by the bifurcation of the colpi. *Insulapollenites* differs from *Cupanieidites* Cookson & Pike 1954 and *Duplopollis* Krutzsch 1959 in having islands (operculae) at the equator of the grain as well as at the poles.

Insulapollenites rugulatus Leffingwell 1971

Plate 7, figure 8

Duplopollis sp. Elsik, 1968b, p. 638, pl. 34, fig. 6.

Insulapollenites rugulatus Leffingwell, 1971, p. 48, pl. 9, figs. 11-12; Pocknall and Nichols, 1996, p. 20-21, pl. 5, figs. 1-4.

Cupanieidites? sp. Frederiksen, 1979, p. 160, pl. 4, figs. 11-12.

Dimensions. Equatorial diameter 28 – 31 μm (two specimens measured). Leffingwell (1971) gave a range of 26.5 -34 μm for the protologue specimens.

Remarks. In addition to the morphological features outlined in the genus remarks, this species is characterised by its rugulate to microreticulate exine ornamentation. The morphology and biogeography of this taxon was discussed in detail by Pocknall

and Nichols (1996).

Botanical affinity. Pocknall and Nichols (1996) suggested Sapindaceae or Myrtaceae as possible affinities for this taxon.

Occurrence. Occurred in relative abundances of <1% in 19/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation of Texas. This taxon is considered to be a reliable Paleocene indicator taxon on the US Gulf Coast (Frederiksen, 1998); the single specimen recovered from the Hatchetigbee Formation is therefore probably reworked.

Genus *Platanus* Linnaeus

Remarks. Pollen of extant *Platanus* is tricolpate with wide, gaping colpi that may have beaded or ragged edges, and a microreticulate exine. *Platanus* pollen differs from that of the form genus *Tricolpites* primarily in being larger, and from *Retitrescolpites* in having a finer reticulum.

Platanus occidentaloides Frederiksen 1980

Plate 7, figure 9

Tricolpites n. sp. A (microreticulate) Tschudy, 1973a, p. B13, pl. 2, figs. 11-12 only.

Platanus occidentaloides Frederiksen, 1980a, p. 48-49, pl. 10, fig. 19.

Platanus sp. Frederiksen, 1980b, p. 162, pl. 4, fig. 22.

Dimensions. Polar diameter 22 μm (one specimen measured); equatorial diameter 25 – 30 μm , mean 28 μm (four specimens measured). Frederiksen (1980a) gave a range of 26 – 35 μm for the polar diameter of the protologue specimens, and a range of 22 – 35 μm for the equatorial diameter.

Remarks. This taxon represents spheroidal to subprolate pollen with widely gaping colpi that extend 2/3 to 3/4 the length of the grain. The colpi edges are only weakly thickened but are rough and may appear beaded. The sexine is semitectate and microreticulate, with lumina approximately 0.5 µm wide. *Platanus occidentaloides* differs from *Platanus mullensis* Simpson 1961 and *Platanus scotica* Simpson 1961 in being spheroidal to subprolate in shape, rather than prolate. It differs from *Tricolpites asper* in being larger.

Botanical affinity. *Platanus* (Platanaceae). Frederiksen (1980a) likened this species to the extant *Platanus occidentalis* Linnaeus, which differs in being slightly smaller and having slightly shallower colpi.

Occurrence. Occurred in relative abundances of <5% in 2/151 samples, in the Zilpha Formation on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Genus *Retitrescolpites* Sah 1967

Remarks. See Chapter 4 for genus remarks and type species.

Retitrescolpites anguloluminosus (Anderson 1960) Frederiksen 1979

Plate 7, figures 10-11

Tricolpites anguloluminosus Anderson, 1960, p. 26, pl. 6, figs. 15-17; pl. 8, figs. 17-18.

Tricolpopollenites anguloluminosus (Anderson) Elsik, 1968b, p. 624, pl. 24, figs. 15-16; pl. 25, fig. 1.

Retitrescolpites anguloluminosus (Anderson) Frederiksen, 1979, p. 139, pl. 1, fig. 13.

Dimensions. Equatorial diameter 31 µm (one specimen measured). Anderson (1960)

gave a range of 20 – 33 μm for the protologue specimens.

Remarks. This species includes pollen with a reticulate exine with thin muri and angular lumina that are $\sim 2\ \mu\text{m}$ wide. The amb is circular to trilobate in shape and the grain is spherical in equatorial view. The colpi gape open and extend 1/2 to 2/3 the distance to the pole. The colpi are bordered by muri, which form a margo. *Retitrescolpites catenatus* Pocknall & Nichols 1996 differs from *Retitrescolpites anguloluminosus* in having a more complex, heterobrochate reticulation pattern, in which small lumina border larger lumina in a chain-like pattern.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of $<1.7\%$ in 37/151 samples, from the Naheola to the Tusahoma formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

“Retitrescolpites sp.1” of Frederiksen 1983

Plate 7, figure 14

Retitrescolpites sp. 1 Frederiksen in Frederiksen et al., 1983, p. 57-58, pl. 16, figs. 20-21.

Dimensions. Equatorial diameter 41 μm (one specimen measured). Frederiksen (in Frederiksen et al 1983) gave a diameter of 43 μm for his specimen.

Remarks. Frederiksen (in Frederiksen et al., 1983) documented one specimen of this morphotype from the Middle Eocene of San Diego, California. The amb is circular with gaping colpi that extend $\sim 1/2$ way from the equator to the poles. The colpi are not bordered by thickened or thinned margins. The exine is coarsely reticulate with lumina 2 – 3 μm wide and muri $\sim 0.5\ \mu\text{m}$ wide. The muri are baculate in optical section and simplibaculate in plan view. Two other morphotypes assignable to *Retitrescolpites* that Frederiksen (in Frederiksen et al., 1983) described from the same material differed in being more coarsely reticulate and larger. *Retitrescolpites*

anguloluminosus differs in being smaller and more finely reticulate.

Botanical affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast.

Genus *Tricolpites* Cookson 1947 ex Couper 1953 emend. Potonié 1960

Remarks. See Chapter 4 for genus remarks and type species.

Tricolpites asper Frederiksen 1978

Plate 7, figure 17

Tricolpopollenites hians (Stanley 1965) Elsik, 1968b, p. 622-624, pl. 24, figs. 5-7, 9 only.

Tricolpites n. sp. A (microreticulate) Tschudy, 1973a, p. B13, pl. 2, figs. 9-10 only.

Tricolpites asper Frederiksen, 1978, p. 694, figs. 11-s; Frederiksen, 1979, p. 139, pl. 1, fig. 12; Harrington, 2003b, pl. 1, figs. 24-25; Jardine and Harrington, 2008, pl. 3, fig. 2.

Dimensions. Polar diameter 17 – 21 μm , mean 18 μm (three specimens measured); equatorial diameter 14 – 20 μm , mean 17 μm (nine specimens measured). Frederiksen (1978) gave a range of 16 – 18 μm for the polar diameter of the protologue specimens, and a range of 17 – 25 μm for the equatorial diameter.

Remarks. This species is distinguished by its small size and shallow, gaping colpi that have ragged edges. The reticulum is muri-clavate with lumina $\sim 0.25 \mu\text{m}$ wide. The exine thins towards the colpi margins. *Tricolpites asper* differs from *Tricolpites hians* in having shallower colpi with rough edges, and from *Platanus occidentaloides* in being smaller and having a finer reticulum.

Botanical affinity. Unknown. The similarity to *Platanus* pollen is suggestive of a

relationship, but this is not certain given the much smaller size of *Tricolpites asper*.

Occurrence. Occurred in relative abundances of <22% in 88/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Tricolpites crassus Frederiksen 1979

Plate 7, figure 18

Tricolpites crassus Frederiksen, 1979, p. 139, pl. 1, figs. 7-8; Frederiksen, 1980b, p. 162, pl. 2, fig. 16.

Dimensions. Equatorial diameter 20 μm (one specimen measured). Frederiksen (1979) gave a range of 16 – 22 μm for the protologue specimens.

Remarks. This taxon is oblate with a triangular amb. The colpi are very short and only 1 – 3 μm deep. The exine is 2 – 3 μm thick in the intercolpium, and thins to less than 1 μm at the colpi. The sexine is internally structureless to indistinctly columellate, and microreticulate in plan view. *Tricolpites crassus* differs from other species in this genus by its thick exine and very short and shallow colpi.

Botanical affinity. Unknown.

Occurrence. One specimen recorded from the base of the Tusahoma Formation on the eastern Gulf Coast.

Tricolpites hians Stanley 1965

Plate 7, figure 19

Tricolpites hians Stanley, 1965, p. 321, pl. 47, fig. 24-27; Elsik, 1968b, p. 622-624, pl. 24, figs. 1-4 only; Pocknall and Nichols, 1996, p. 17-18, pl. 4, fig. 18; Jardine and Harrington, 2008, pl. 3, fig. 3.

Tricolpites parvus Stanley, 1965, p. 322, pl. 47, fig. 28-31.

Dimensions. Equatorial diameter 22 – 34 μm , mean 29 μm (eight specimens measured).

Remarks. This taxon includes tricolpate pollen with a subcircular to triangular amb and gaping, deeply incised colpi. The exine is microreticulate, with lumina less than 0.5 μm wide. Here I follow Pocknall and Nichols (1996) in treating *Tricolpites hians* and *Tricolpites parvus* as being synonymous, the only difference between them being in the thickness of the nexine. *Tricolpites hians* differs from both *Tricolpites asper* and *Platanus occidentaloides* in having more deeply incised colpi with straight rather than ragged edges, and in overall size.

Botanical affinity. Pocknall and Nichols (1996) suggested a possible affinity with Platanaceae.

Occurrence. Occurred in relative abundances of <27% in 84/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Tricolpites reticulatus Cookson 1947 ex Couper 1953

Plate 7, figure 20

Tricolpites reticulatus Cookson, 1947, p. 134, pl. 15, fig. 45 ex Couper, 1953, p. 61; Frederiksen, 1988, pl. 7, figs. 11-12.

Dimensions. Equatorial diameter 19 – 25 μm (two specimens measured).

Remarks. *Tricolpites reticulatus* has a lobate amb with strongly convex mesocolpia, and a very fine microreticulate exine. The colpi are 1/2 to 3/4 the length of the grain, and are only lightly bordered by nexinal thickenings. *Tricolpites reticulatus* differs from *Tricolpites hians* primarily in having convex rather than straight mesocolpia, and

slightly concave sides to the colpi in polar view. *Tricolpites interangulus* Newman 1965 is similar to *Tricolpites reticulatus* but has equatorial exinal thickenings at the colpi (Frederiksen in Frederiksen et al., 1983).

Botanical affinity. Similar to pollen of extant *Gunnera* Linnaeus (Gunneraceae) (Leffingwell, 1971; Srivastava, 1972).

Occurrence. Occurred in relative abundances of <1% in 6/151 samples, in the Hatchetigbee and Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Tricolpopollenites* Pflug & Thomson in Thomson & Pflug 1953

Remarks. See Chapter 4 for genus remarks and type species.

Tricolpopollenites geranioides (Couper 1960) Elsik 1968

Plate 8, figures 5-6

Tricolpites geranioides (Couper 1960) Elsik, 1968b, p. 624, pl. 25, figs. 3-7.

Rousea sp. Jardine and Harrington, 2008, pl. 2, fig. 25.

Retitrescolpites sp. 1. Jardine and Harrington, 2008, p. 195-196, pl. 3, fig. 30.

Tricolpate sp. 1. Jardine and Harrington, 2008, p. 198, pl. 3, fig. 1.

Dimensions. Equatorial diameter 24 – 38 μm , mean 29 μm (nine specimens measured); polar diameter 24 – 29 μm (two specimens measured).

Remarks. *Tricolpopollenites geranioides* includes spheroidal pollen with a convex-triangular to circular amb, and a coarsely reticulate muri-clavate exine. The lumina are 1 – 3 μm wide and variable in shape, the muri are 0.5 – 1 μm wide and simplibaculate, and the exine is ~3 μm thick. The colpi extend 2/3 to 3/4 the length of the grain and are only lightly bordered by thickened margins, if at all. This species

is therefore distinguished by its thick, coarsely reticulate exine and spheroidal shape. In my material the size range for this taxon is quite large, but all specimens share the same distinctive exine structure and sculpture. *Retitrescolpites anguloluminosus* is more finely reticulate, and “*Retitrescolpites* sp.1” of Frederiksen 1983 is larger, has a coarser reticulum comprising baculate, rather than clavate, elements. *Reticulataepollis* sp. of Frederiksen (1979) is similar in terms of grain shape and style of reticulation, but has only very short and shallow colpi. Re-examination of samples from the Red Hills Mine revealed that specimens assigned to three informal taxa in Jardine and Harrington (2008) all in fact belong to *Tricolpopollenites geranioides*.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1.1% in 15/151 samples, in the Nanafalia and Tusahoma formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

TRICOLPORATE POLLEN

Genus *Aesculiidites* Elsik 1968

Type species. *Aesculiidites circumstriatus* (Fairchild, in Stover, Elsik and Fairchild 1966) Elsik 1968.

Remarks. This form genus includes tricolpate to tricolporate pollen with a circumstriate exine ornamentation. The striations may be formed of punctae, granules, or aligned lumina and muri in a reticulate ornamentation. The grains are prolate spheroidal to prolate. *Aesculiidites* differs from *Ailanthipites* in having striae that run parallel to the equator and circle the pole, rather than having striae that run parallel to the polar axis.

Aesculiidites circumstriatus (Fairchild in Stover et al 1966) Elsik 1968

Plate 8, figures 10-12

Tricolpites circumstriatus Fairchild in Stover et al., 1966, p. 5, pl. 2, figs. 3-7.

Aesculiidites circumstriatus (Fairchild) Elsik, 1968b, p. 632-634, pl. 27, fig. 10-18; pl. 28, fig. 1-7; Tschudy, 1973a, p. B13-B14, pl. 2, fig. 13-15; Frederiksen, 1980b, p. 165, pl. 2, fig. 32; Pocknall and Nichols, 1996, p. 18, pl. 4, fig. 19-20.

Dimensions. Polar diameter 19 – 20 μm (five specimens measured); equatorial diameter 15 – 17 μm , mean 16 μm (seven specimens measured). Fairchild (in Stover et al. 1966) gave a range of 18 – 22 μm for the polar diameter of the protologue specimens, and a range of 14 – 16 μm for the equatorial diameter.

Remarks. The major morphological features of this taxon have been outlined in the genus remarks. Additional details are that the colpi are very long and almost reach the poles, and in some specimens a small trilete mark, offset 60° to the colpi, is visible at the poles. In my material most of the grains are colporate; the pores in this species are distinctly lalongate and elliptical in shape. The striate sculpture varies from punctate to muri-clavate reticulate in my specimens. The striate nature of the ornamentation was sometimes indistinct but always visible under high-power magnification with oil immersion. This species differs from *Aesculipollis wyomingensis* Pocknall & Nichols 1996 in lacking granules on the colpi, in having a thicker and more distinctly sculptured exine, and in having lalongate rather than circular ora.

Botanical affinity. Possibly Hippocastanoideae of the Sapindaceae (Elsik, 1968b; Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <10% in 27/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Ailanthipites* Wodehouse 1933

Type species. *Ailanthipites berryi* Wodehouse 1933.

Remarks. This form genus encompasses spheroidal to prolate pollen with a foveo-striate exine ornamentation. The foveolae are linearly arranged, and aligned subparallel to each other. *Aesculiidites* has elements linearly aligned with the equatorial axis and circling the poles, *Rhuspollenites* Thielle-Pfeiffer 1980 is retistriate rather than foveo-striate, and *Striatopollis* is truly striate (Nichols, 2010).

Ailanthipites berryi Wodehouse 1933

Plate 8, figures 13-14

Ailanthipites berryi Wodehouse, 1933, p. 512, fig. 44; Frederiksen, 1979, p. 161, pl. 4, figs. 19-20; Frederiksen, 1980a, p. 57-58, pl. 14, figs. 3-6; Frederiksen in Frederiksen et al., 1983, p. 81, pl. 22, figs. 1-2; Nichols, 2010, p. 69, pl. 16, figs. 6-10

Ailanthipites sp. cf. *A. berryi* Wodehouse. Pocknall and Nichols, 1996, p. 21, pl. 5, figs. 5-7 only.

Dimensions. Polar diameter 25 – 32 μm , mean 29 μm ; equatorial diameter 18 – 24 μm , mean 21 μm (eight specimens measured). Wodehouse (1933) gave a range of 26 – 30 μm for the polar diameter of the protologue specimens, and a range of 20 – 25 μm for the equatorial diameter.

Remarks. *Ailanthipites berryi* represents spheroidal to prolate, tricolporate pollen with distinct, lalongate ora and a foveo-striate exine where the striations run subparallel to the polar axis. This taxon differs from *Ailanthipites nonprolatus* Frederiksen in Frederiksen et al 1983 in its larger size, and from *Ailanthipites marginatus* Frederiksen in Frederiksen et al 1983 in lacking distinctly thickened colpi margins.

Botanical affinity. Similar grains are produced by members of the Anacardiaceae,

Fabaceae, Sapindaceae, and Simaroubaceae (Frederiksen, 1980a; Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <8% in 19/151 samples, from the Naheola to the Tallahatta formations on the eastern Gulf Coast. This taxon is very rare in the Paleocene, but becomes more common in the Eocene. It is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Genus *Boehlensipollis* Krutzsch 1962 emend. Frederiksen in Frederiksen et al. 1983

Type species. *Boehlensipollis hohlii* Krutzsch 1962.

Remarks. *Boehlensipollis* accommodates oblate pollen with a concave-triangular to slightly convex-triangular amb, and narrow colpi that extend to or nearly to the pole on at least one hemisphere. This genus therefore includes both isopolar and heteropolar grains. The ora are large, circular and atriate. *Psittacopollis* van Ameron 1965 is similar but the ora are not atriate.

Boehlensipollis minimus (Leffingwell 1971) Pocknall & Nichols 1996

Plate 8, figures 16-17

Syncolporites minimus Leffingwell, 1971, p. 49-50, pl. 9, figs. 6-8

Boehlensipollis minimus (Leffingwell) Pocknall and Nichols, 1996, p. 21-22, pl. 5, fig. 9-14.

Dimensions. Equatorial diameter 14 μm (one specimen measured). Leffingwell (1971) gave a range of 15.5 – 23.3 μm for the protologue specimens.

Remarks. This species is characterised by its very small size and the heteropolar

nature of the colpi. On one hemisphere the colpi are long and extend to, or almost to, the pole, whereas on the other hemisphere the colpi extend less than one third the radius of the grain. The colpi are unbordered, and the ora are atriate to indistinctly vestibulate. The sexine is scabrate to finely granulate. *Boehlensipollis verrucata* and *Boehlensipollis granulata* Frederiksen in Frederiksen et al 1983 are both much larger than *Boehlensipollis minimus*.

Botanical affinity. Sapindaceae (Pocknall and Nichols, 1996).

Occurrence. One specimen recorded, from the Hatchetigbee Formation of the eastern Gulf Coast.

Boehlensipollis verrucata Frederiksen 1988

Plate 8, figure 18

Boehlensipollis sp. 2. Frederiksen in Frederiksen et al., 1983, p. 62, pl. 17, figs. 26-28.

Boehlensipollis verrucata Frederiksen, 1988, p. 54-55, pl. 10, figs. 9-10.

Dimensions. Equatorial diameter 39 μm . Frederiksen (1988) gave a range of 33 – 39 μm for the protologue specimens.

Remarks. *Boehlensipollis verrucata* includes large, heteropolar grains with a thick, columellate and densely verrucate exine. On one hemisphere the colpi extend to the pole, and on the other the colpi extend 1/3 to 1/2 the grain radius. The sexine appears coarsely clavate in optical section, and shows a true negative reticulum in plan view. Frederiksen (1988) erected this species based on two specimens; one from the Middle Eocene of Alabama, and one from the Middle Eocene of California. Although the single specimen in my material is degraded, with much of the sexine pulled away from the nexine, it demonstrates all the features of Frederiksen's (1988) grains, and extends the range of this taxon on the Gulf Coast down into the Early Eocene Hatchetigbee Formation. *Boehlensipollis verrucata* can be distinguished from other

species in this genus by its verrucate exine ornamentation.

Botanical affinity. Unknown.

Occurrence. One specimen recorded from the Hatchetigbee Formation on the eastern Gulf Coast. This taxon is known to range up into the upper part of the Claiborne Group (Frederiksen, 1988).

Genus *Bombacacidites* Couper 1960

Remarks. See Chapter 4 for genus remarks and type species.

Bombacacidites nacimientoensis (Anderson 1960) Elsik 1968b

Plate 8, figure 19

Bombacacidites nacimientoensis Anderson, 1960, p. 23, pl. 8, fig. 13.

Bombacacidites nacimientoensis (Anderson) Elsik, 1968b, p. 620, pl. 22, fig. 1-2, 4; Frederiksen, 1979, p. 159; Frederiksen, 1980a, p. 59, pl. 14, fig. 15; Frederiksen in Frederiksen et al., 1983, p. 77-79, pl. 21, fig. 12-13, 15-17; Frederiksen, 1988, pl. 15, fig. 11-12; Jaramillo and Dilcher, 2001, p. 113, pl. 6, fig. 16-17.

Bombacacidites nacimientensis (Anderson) Srivastava, 1972, p. 242.

Dimensions. Equatorial diameter 29 μm (one specimen measured). Anderson (1960) gave a range of 35 – 39 μm for the protologue specimens. Frederiksen (in Frederiksen et al., 1983) gave a range of 28 – 53 μm for specimens from California and the eastern US Gulf Coast.

Remarks. This species is characterised by a triangular amb with straight to slightly convex sides, and a reticulate exine that is strongly heterobrochate between the apocolpia and mesocolpia. Although this taxon has frequently been used as a

generalised morphospecies for straight-sided triangular *Bombacacidites*-types (Frederiksen in Frederiksen et al., 1983), the lumina at the poles should be at least 1.5 μm wide, and are much finer (typically $\leq 0.5 \mu\text{m}$) at the corners. Similar specimens that have polar lumina of $\sim 1 \mu\text{m}$ are here assigned to “*Bombacacidites* sp.1” of Frederiksen 1988. The angles of the grain may be wide or narrow; most of the specimens in my samples have wide, well-rounded angles, similar to the specimen illustrated by Frederiksen (1988). *Bombacacidites fereparilis* Frederiksen in Frederiksen et al 1983 is less coarsely reticulate at the poles and less heterobrochate, having lumina that are 1 μm at the poles, and 0.7 μm at the corners.

Botanical affinity. Probably Bombacoideae of the Malvaceae *s.l.* (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of $<0.7\%$ in 11/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This species is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Bombacacidites reticulatus Krutzsch 1961

Plate 8, figure 20

Bombacacidites reticulatus Krutzsch, 1961, p. 315. pl. 3, fig. 53-54; Frederiksen, 1980b, p. 170, pl. 3, fig. 28.

Tiliaepollenites reticulatus Groot and Groot, 1962, p. 168, pl. 30, fig. 31-33.

Bombacacidites reticulatus (Groot & Groot) Srivastava, 1972, p. 242, pl. 8, fig. 3-6.

Intratropipollenites reticulatus (Groot & Groot) Frederiksen, 1979, pl. 4, fig. 2.

Dimensions. Equatorial diameter 26 – 31 μm , mean 28 μm (three specimens measured). Groot and Groot (1962) gave a range of 27 – 35 μm for *Tiliaepollenites reticulatus*.

Remarks. This species of *Bombacacidites* is distinguished by its circular to strongly convex-triangular amb. The size of the lumina at the poles and grain angles is variable from grain to grain, but in my material the lumina on the apocolpia are 1 – 3 μm wide, and at the mesocolpia they are $<0.5 \mu\text{m}$ wide. This is therefore a heterogeneous species, but it differs from other *Bombacacidites* types in its circular to nearly circular, rather than triangular, amb.

Botanical affinity. Probably Bombacoideae of the Malvaceae *s.l.* (Frederiksen in Frederiksen et al., 1983).

Occurrences. Occurred in relative abundances of $<3.5\%$ in 40/151 samples, from the Porters Creek to the base of the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

“*Bombacacidites* sp.1” of Frederiksen 1988

Plate 8, figure 21

Bombacacidites sp.1. Frederiksen, 1988, p. 58, pl. 15, fig. 6-10.

Dimensions. Equatorial diameter 23 – 31 μm , mean 26 μm (four specimens measured). Frederiksen (1988) gave a range of 22 – 28 μm for the protologue specimens.

Remarks. Pollen assignable to this taxon are similar to *Bombacacidites nacimientoensis*, except in that the lumina on the apocolpia are $\sim 0.8 - 1 \mu\text{m}$ wide, rather than at least 1.5 μm wide. As with *B. nacimientoensis* the lumina on the mesocolpia are much smaller, and in my specimens are typically $\sim 0.2 \mu\text{m}$ wide. The amb is triangular with straight to slightly convex sides, and wide, well-rounded angles. Both *B. fereparilis* Frederiksen in Frederiksen et al 1983 and *B. hungaricus* Kedves 1974 have polar lumina of $\sim 1 \mu\text{m}$, but neither are so finely reticulate at the grain angles.

Botanical affinity. Probably Bombacoideae of the Malvaceae *s.l.* (Frederiksen in

Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <2.4% in 12/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Caprifoliipites* Wodehouse 1933

Remarks. See Chapter 4 for genus remarks and type species.

Caprifoliipites spp.

Plate 9, figures 2-5

?*Caprifoliipites* sp. 1. Jardine and Harrington, 2008, p. 194, pl. 3, fig. 5.

?*Caprifoliipites* sp. 2. Jardine and Harrington, 2008, p. 194, pl. 3, fig. 6.

Dimensions. Polar diameter 13 – 19 μm , mean 16 μm (eight specimens measured); equatorial diameter 12 – 21 μm , mean 16 μm (14 specimens measured).

Remarks. This taxon comprises a heterogeneous group of small, prolate to oblate spheroidal, microreticulate grains with indistinct ora. All are muri-clavate microreticulate, and most have long colpi that almost reach the poles. It was not possible to consistently separate these specimens into meaningful morphotypes, and so I have counted them as one group. Some may represent *Caprifoliipites tantulus* Frederiksen 1980. Specimens assigned to *Horniella* spp. are similar, but are exclusively prolate to prolate spheroidal and have more distinct ora.

Botanical affinity. Some specimens may belong to the Caprifoliaceae (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <5% in 28/151 samples, from the

Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Cupuliferoipollenites* Potonié 1951 ex Potonié 1960

Type species. *Cupuliferoipollenites pusillus* (Potonié 1934) Potonié 1960.

Remarks. *Cupuliferoipollenites* accommodates small, prolate spheroidal to prolate pollen. The exine is smooth and not columellate; only a faint infratexture is present. The colpi are long and the pores are small and circular. This genus is most similar to *Cupuliferoideaipollenites*, but differs in being tricolporate rather than tricolpate.

Cupuliferoipollenites spp.

Plate 9, figures 6-9

Tricolporopollenites cingulum (Potonié 1934) Thomson & Pflug 1953. Elsik, 1968b, p. 628, pl. 27, fig. 8; Tschudy, 1973a, p. B17, pl. 4, figs. 24-28.

Cupuliferoipollenites spp. Frederiksen, 1980a, p. 50, pl. 11, figs. 9-11; Frederiksen, 1980b, p. 164, pl. 2, figs. 21-23; Frederiksen in Frederiksen et al., 1983, p. 59, pl. 17, figs. 3-5.

Dimensions. Polar diameter 12 – 21 μm , mean 15 μm ; equatorial diameter 7 – 14 μm , mean 11 μm (17 specimens measured).

Remarks. Pollen grains assigned to *Cupuliferoipollenites* spp. are small, prolate spheroidal to prolate, and have a smooth exine. Exine thickness varies from 0.5 – 2 μm thick, with the sexine being the same to twice the thickness of the nexine. Most specimens probably either represent *Cupuliferoipollenites pusillus* (Potonié 1934) Potonié 1960 or *Cupuliferoipollenites insleyanus* (Traverse 1955) Potonié 1960,

the former species representing the prolate forms and the latter representing the prolate spheroidal to subprolate forms. However, in reality there is a morphological continuum in grain shape between these types, and given the difficulty in consistently separating specimens into species, especially when variation in exine thickness is taken into account, I have counted these together in one group. *Siltaria hanleyi* Pocknall & Nichols 1996 is similar to the more prolate specimens of *Cupuliferoipollenites* spp., but differs in being distinctly columellate.

Botanical affinity. Probably Fagaceae, or possibly Fabaceae (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <27% in 86/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Genus *Favitricolporites* Sah 1967 emend. Srivastava 1972

Remarks. See Chapter 4 for genus remarks and type species.

Favitricolporites baculoferus (Pflug in Thomson & Pflug 1953) Srivastava 1972

Plate 9, figures 10-11

Tricolporopollenites baculoferus Pflug in Thomson and Pflug, 1953, p. 105, pl. 14, figs. 4-8 only; Elsik, 1968b, p. 626, pl. 25, figs. 9-11; pl. 26, figs. 1-4.

Favitricolporites baculoferus (Pflug) Srivastava, 1972, p. 256, pl. 14, figs. 7-11; pl. 15, figs. 1-7, pl. 16, figs. 1-9; Frederiksen, 1979, p. 160-161; Jardine and Harrington, 2008, pl. 3, fig. 12.

Tricolporopollenites spp. of the *T. baculoferus* type. Tschudy, 1973a, p. B12, pl. 1, figs.

21-26.

Dimensions. Polar diameter 23 – 44 μm , mean 32 μm (10 specimens measured); equatorial diameter 18 – 36 μm , mean 26 μm (13 specimens measured). Pflug (in Thomson and Pflug, 1953) gave a range of 30 – 50 μm for the polar diameter of the protologue specimens. For specimens of *Favitricolporites baculoferus* from the Naheola Formation of Alabama, Srivastava (1972) gave a range of 22 – 34 μm for the polar diameter, and 18 – 27 μm for the equatorial diameter.

Remarks. The major morphological features of this taxon have been described in the genus remarks. The sexine comprises pila partially fused into a retipilate sculpture, with lumina less than 1 μm in diameter. The amb is \pm circular, and in equatorial view the grain is subprolate to suboblate. The ora range from indistinct to distinct, and may be hard to distinguish, especially when the grain is preserved in polar view. I have assigned similar forms that are truly colpate to *Tricolpites* sp. 4. *Favitricolporites* sp. 1 is smaller and has a finer reticulum; *Favitricolporites* sp. 2 has a coarser reticulum and more distinct ora.

Botanical affinity. Unknown. Lobreau-Callen and Srivastava (1974) suggested an affinity with *Platea* (Icacinaeae), although they themselves noted several deviations in grain and aperture size between most specimens of *Favitricolporites baculoferus* and modern *Platea* pollen.

Occurrence. Occurred in relative abundances of <19% in 120/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Holkopollenites* Fairchild in Stover et al. 1966

Type species. *Holkopollenites chemardensis* Fairchild in Stover et al. 1966.

Remarks. This genus is characterised by nexinal channels that in polar view run

± parallel to the grain sides. The grain is oblate spheroidal and the amb is obtuse-straight-triangular to obtuse-concave-triangular. The colpi are deeply incised and are bordered by thickened margins that extend the full length of the colpi; the ora are lalongate and inconspicuous. The sexine is punctate to microreticulate. *Holkopollenites* differs from *Nyssapollenites* primarily by the presence of distinct nexinous channels, and in having uniformly thickened colpi margins (Srivastava, 1972).

Holkopollenites chemardensis Fairchild in Stover et al. 1966

Plate 9, figures 16-19

Holkopollenites chemardensis Fairchild in Stover et al., 1966, p. 6, pl. 1, fig. 11; pl. 2, figs. 8-9; Srivastava, 1972, p. 258, pl. 17, fig. 1-15; pl. 18, figs. 1-13; Frederiksen, 1980b, p. 167, pl. 3, fig. 22.

Cf. *Holkopollenites chemardensis* Fairchild. Elsik, 1968b, p. 636, pl. 28, figs. 16-18; pl. 29, figs. 1-2; pl. 30, figs. 1-3.

Dimensions. Polar diameter 25 – 31 µm, mean 27 µm (three specimens measured); equatorial diameter 23 – 34 µm, mean 28 µm (14 specimens measured). Fairchild (in Stover et al., 1966) gave a range of 31 – 40 µm for the equatorial diameter of the protologue specimens; Srivastava (1972) gave a range of 17 – 27 µm for specimens from the Naheola Formation of Alabama.

Remarks. The major defining features of this species have been listed in the genus remarks. The nexinal channels range from distinct to weakly developed. Nexinal channels are also a feature of cf. *Symplocoipollenites* Elsik 1968b, and to an extent these taxa intergrade morphologically (e.g. Plate 9, figure 19, and plate 12, figure 18). In cf. *Symplocoipollenites* the channels are typically less distinct than in *Holkopollenites chemardensis*, and are more variable in their orientation. These two taxa can also be distinguished by the deeply incised and thickened colpi characteristic

of *Holkopollenites chemardensis*, and the more distinct, vestibulate pore and convex-triangular amb in cf. *Symplocoipollenites*.

Botanical affinity. Unknown.

Occurrences. Occurred in relative abundances of <23% in 80/151 samples, from the Porters Creek to the Tuscaloosa formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Horniella* Traverse 1955

Remarks. See Chapter 4 for genus remarks and type species.

Horniella brevicolpata Frederiksen in Frederiksen et al. 1983

Plate 9, figure 20

Horniella brevicolpata Frederiksen in Frederiksen et al., 1983, p. 70, pl. 19, figs. 25-27, 34.

Dimensions. Polar diameter 44 – 51 μm , mean 47 μm ; equatorial diameter 23 – 31 μm , mean 27 μm (four specimens measured). Frederiksen (in Frederiksen et al., 1983) gave a range of 34 – 57 μm for the polar diameter of the protologue specimens.

Remarks. *Horniella brevicolpata* accommodates prolate to perprolate retistriate grains. The colpi are typically shallow and under 2/3 the length of the grain, although folding parallel to the polar axis may make the colpi appear longer than they actually are. The ora are distinct and round to lalongate. The exine is finely retistriate with lumina 0.5 – 1.5 μm wide and elongate parallel to the polar axis. *Ailanthipites berryi* is foveo-striate and encompasses smaller grains that are prolate to spheroidal. *Rhoipites latus* is smaller, has thicker exine, and has more distinct, relatively longer colpi that

are bordered by thickenings.

Botanical affinity. Possibly *Triumfetta* Linnaeus or *Grewia* Linnaeus (both Grewioideae of the Malvaceae s.l.) (Frederiksen in Frederiksen et al., 1983).

Occurrence. Occurred in relative abundances of <1.4% in 2/151 samples, from the Hatchetigbee and Zilpha formations on the eastern Gulf Coast. This taxon has not previously been recorded from the US Gulf Coast.

Horniella spp.

Plate 9, figures 26-28

Dimensions. Polar diameter 14 – 28 μm , mean 22 μm ; equatorial diameter 9 – 22 μm , mean 17 μm (six specimens measured).

Remarks. This taxon includes small, prolate to prolate spheroidal microreticulate grains with long colpi and distinct, lalongate to round ora. The colpi are only weakly bordered, if at all. It proved difficult to consistently separate these forms into specific taxa, so I have counted them together as one group. Similar forms with indistinct ora were counted as *Caprifoliipites* spp.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <2.1% in 22/151 samples, from the Naheola to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Ilexpollenites* Thiergart 1937 ex. Potonié 1960

Type species. *Ilexpollenites iliacus* (Potonié 1931) Potonié 1960.

Remarks. This form genus includes tricolporate pollen with a sexine comprising free-standing pilae or clavae, which may vary in size and morphology across the grain.

It therefore differs from *Favitricolporites* in having sculptural elements that are free-standing, rather than fused together into a loose reticulum.

Ilexpollenites spp. cf. *Ilex media* (Pflug & Thomson 1953) Frederiksen 1980

Plate 9, figures 29-30

Ilexpollenites spp. Tschudy, 1973a, p. B15, pl. 3, figs. 10-12.

Ilex media (Pflug & Thomson in Thomson & Pflug 1953) Frederiksen, 1980a, p. 53-54, pl. 12, figs. 15-16; Frederiksen in Frederiksen et al., 1983, p. 67, pl. 18, figs. 36-37.

Dimensions. Polar diameter 22 – 25 μm , mean 23 μm (four specimens measured); equatorial diameter 19 – 26 μm , mean 22 μm (seven specimens measured).

Remarks. Grains assigned to this morphotype are subprolate to oblate spheroidal. Grains in polar view had deeply incised and gaping colpi with a lobate amb. The clavae are up to 3 μm long, and densely cover the grain surface. Most of these specimens probably represent *Ilex media* (Pflug & Thomson 1953) Frederiksen 1980a. Some may represent *Ilex infissa* Frederiksen 1980a, but poor preservation or orientation of some of the grains meant that the slit-like longitudinal ora diagnostic of that species could not be observed.

Botanical affinity. At least in part *Ilex* Linnaeus (Aquifoliaceae) (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <8% in 9/151 samples, in the Tallahatta and Zilpha formations on the eastern Gulf Coast. *Ilex media* is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Genus *Intratriporopollenites* Pflug & Thomson in Thomson & Pflug 1953 emend.

Nichols 2010

Type species. *Intratriporopollenites instructus* (Potonié 1931) Thomson & Pflug 1953.

Remarks. As emended by Nichols (2010), this genus includes pollen with three or four brevicolporate apertures. The ora are vestibulate and endannulate; the colpi rarely extend beyond the endannuli. The grain is oblate to peroblate, and the amb is circular to broadly rounded triangular, with the apertures located between rather than at the grain angles (=planaperturate). The exine is tectate and granulate, and may also be punctate and/or infrareticulate. This emendation broadened the diagnosis from that of Mai (1961), to include forms that depart from the morphology of extant *Tilia*, especially in including tetracolporate forms. Most species included in *Intratriporopollenites* probably belong to Tilioideae or its ancestral stock, but may also represent ancestors of the extant subfamily Sterculioideae (Nichols, 2010). *Bombacacidites* differs in having ora that are not vestibulate, and in being suprareticulate and heterobrochate, with wider lumina at the poles than at the grain angles. *Porocolpopollenites* differs in being angulaperturate.

Intratriporopollenites instructus (Potonié 1931) Thomson & Pflug 1953

Plate 9, figure 31

Tiliae-pollenites intructus Potonié, 1931c, p. 556, fig. 9.

Intratriporopollenites instuctus (Potonié) Thomson and Pflug, 1953, p. 89, pl. 10, figs. 14-23.

Tilia instructa (Potonié) Frederiksen, 1980a, p. 59, pl. 14, fig. 21-22.

Dimensions. Equatorial diameter 34 – 35 μm (two specimens measured). Potonié (1931c) gave a range of 34 – 42 μm for the protologue specimens.

Remarks. This species includes rounded-triangular to subcircular triaperturate grains with well-developed semi-circular endannuli 2 - 3 μm deep. The colpi are long for this genus and may extend 1/2 to 2/3 the way to the poles. The exine is 1 – 2 μm thick and is distinctly columellate and infrareticulate, with lumina 0.5 – 1 μm wide. The surface of the grain is tectate and granulate.

Botanical affinity. Probably Tilioideae of the Malvaceae *s.l.* Frederiksen (1980a) transferred this species to the extant genus *Tilia* Linnaeus.

Occurrence. Occurred in relative abundances of <5% in 6/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group on the US Gulf Coast (Frederiksen, 1980a).

Intratropollenites pseudinstructus Mai 1961

Plate 10, figure 1

Intratropollenites pseudinstructus Mai, 1961, p. 65, pl. 10, figs. 19-40; Frederiksen, 1979, p. 159, pl. 4, fig. 1.

Intratropollenites pseudinstructus group. Frederiksen, 1988, p. 58, pl. 15, fig. 21-22.

Dimensions. Equatorial diameter 27 – 33 μm , mean 29 μm (seven specimens measured). Mai (1961) gave a range of 26 – 41.5 μm for the protologue specimens.

Remarks. In polar view *Intratropollenites pseudinstructus* has oval to semi-circular endannuli ~1 μm deep, and apertures that gape open slightly. The colpi extend 1 – 2 μm at most beyond the endannulus. The exine is ~1.5 μm thick, and the infrareticulum is distinct and has lumina 0.25 – 0.5 μm wide. This species is therefore similar to *I. instructus* but differs in having narrower and different shaped endannuli, more open colpi, a finer infra-reticulum, and incorporating smaller sized grains. The columellae are also more distinct. Frederiksen (1988) counted this taxon together

with *I. insculptus* Mai 1961, the only difference being that in the latter taxon the sexine does not overhang the apertures. All of the specimens in my material possess overhanging sexine, and so I have assigned them to *I. pseudinstructus* s.s.

Botanical affinity. Probably Tilioideae of the Malvaceae s.l.

Occurrence. Occurred in relative abundances of <3% in 13/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast.

Intratropopollenites vespites (Wodehouse 1933) comb. et emend. Nichols 2010

Plate 10, figures 2-5

Tilia vespites Wodehouse, 1933, p. 516, fig. 49.

Tilia tetraforaminipites Wodehouse, 1933, p. 516, fig. 50.

Porocolpopollenites spp. Elsik, 1968b, p. 634, pl. 28, fig. 15 only.

Intratropopollenites sp. cf. *Tilia tetraforaminipites* Wodehouse. Pocknall and Nichols, 1996, p. 22-23, pl. 5, figs. 23-25; Jardine and Harrington, 2008, pl. 3, fig. 7.

Intratropopollenites vespites (Wodehouse) Krutzsch, 2004, p. 106.

Intratropopollenites vespites (Wodehouse) comb. et emend. Nichols, 2010, p. 78-79, pl. 18, figs. 5-10; pl. 19, figs. 1-6.

Quadrupollis sp. 1. Jardine and Harrington, 2008, p. 195, pl. 4, fig. 12.

Dimensions. Equatorial diameter 23 – 32 μm , mean 27 μm (15 specimens measured). Nichols (2010) gave a range of 25 – 35 μm for specimens from Wodehouse's (1933) original material.

Remarks. As originally described by Wodehouse (1933), *Tilia vespites* and *Tilia tetraforaminipites* differed only in aperture number, with the former being tricolporate, and the latter being tetracolporate. The discovery by Nichols (2010) of specimens of both form species in organic connection unequivocally demonstrated that they together represent a single natural taxon. Nichols (2010) therefore

emended "*Tilia*" *vescipes* to include both tri- and tetra-aperturate specimens, and transferred the species to *Intratropipollenites* to reflect the uncertainty of assigning it to the extant genus, despite its likely tilioideous affinity. Counting these taxa together also brings a degree of uniformity with other zonoaperturate taxa that are not subdivided based on aperture number, such as *Alnus verus*, *Alnus scotica*, *Polyatriopollenites stellatus*, and *Celtis* spp.

This taxon has a circular amb and is peroblate to oblate; rare specimens were observed in oblique or equatorial view rather than the usual polar orientation. The endannuli are 2 – 3 μm deep in polar view and equatorially elongate, and are up to 10 μm wide in equatorial view. The colpi extend $\sim 4 \mu\text{m}$ towards the poles on each hemisphere. The pores are evenly spaced around the equator and protrude slightly from the equatorial outline. The exine is $\sim 1 \mu\text{m}$ thick and granulate; the infrareticulum has lumina $\sim 0.5 \mu\text{m}$ wide. Approximately 75% of specimens were tricolporate. Pocknall and Nichols (1996) recorded rare specimens with five apertures; no such grains were counted in my material. This species differs from *I. instructus* and *I. pseudoinstructus* in including tetracolporate specimens, in the form of the endannulus, which is narrower in polar view and does not form a semi-circle or polar-aligned oval shape, in its protruding ora, and also in its thinner exine. Modern *Tilia* pollen is exclusively tri-aperturate, has a coarser infrareticulate sculpture, and more developed endannuli, and is typically larger in diameter (Nichols, 2010).

Frederiksen (1980b) assigned specimens to *Faguspollenites* spp. that are highly similar to *I. vescipes*, in terms of grain size, exine thickness and the structure of the apertures, including the dimensions and form of the colpi and endannuli. These specimens were described as granulate and columellate but no mention was made of an infrareticulate sculpture. These specimens were also described as spheroidal, where *I. vescipes* is peroblate. However, all of Frederiksen's (1980b) illustrated specimens were in equatorial view, and grains of *I. vescipes* in this orientation may be compressed so as to appear spheroidal in shape (e.g. Plate 10, figure 3).

Faguspollenites spp. of Frederiksen (1980b) may therefore be conspecific with *I. vespipites*.

Botanical affinity. Probably Tilioideae of the Malvaceae s.l. (Nichols, 2010).

Occurrence. Occurred in relative abundances of <4% in 60/151 samples, from the Naheola to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Lanagiopollis* Morley 1982

Remarks. See Chapter 4 for genus remarks and type species.

Lanagiopollis crassa type of Frederiksen 1988

Plate 10, figures 6-8

Lanagiopollis crassa type. Frederiksen, 1988, p. 56, pl. 11, figs. 10-16.

Dimensions. Polar diameter 31 – 41 μm , mean 34 μm ; equatorial diameter 29 – 34 μm , mean 33 μm (three specimens measured).

Remarks. This taxon contains \pm spheroidal grains with an originally psilate exine that often shows pseudosculpturing due to corrosion of the tectum. The exine thickness and type of sculpturing therefore varies considerably from grain to grain; specimens are usually punctate but may also be scabrate, reticulate, foveolate or rugulate (Jaramillo and Dilcher, 2001). The three specimens of *Lanagiopollis crassa* type in my material are all punctate or microreticulate. The sexine is distinctly columellate, the colpi are narrow and unbordered, and the ora are narrow, alongate and endannulate. The endannuli are formed by a gradual thickening of the nexine towards the colpi, which is indicative of *Pelliceria* pollen as opposed to *Alangium*, in

which the nexine thins towards the colpi. As my specimens were all orientated in equatorial view this diagnostic feature could not be observed. My specimens match well with the description and illustrations given by Frederiksen (1988), although whether these are conspecific with *Lanagiopollis crassa* s.s., as recorded by van der Hammen & Wymstra (1964) and Jaramillo and Dilcher (2001), is not clear due to the potential variability of this taxon. *Lanagiopollis cribellata* is similar to punctate/microreticulate specimens of *Lanagiopollis crassa* but has a thinner wall and thickened margins bordering the colpi. *Lanagiopollis eocaenica* type is muri-clavate reticulate and has lightly bordered colpi.

Botanical affinity. Probably *Pelliceria*, or at least a member of the Theaceae (Jaramillo and Dilcher, 2001).

Occurrence. Three specimens recorded in the Tallahatta Formation on the eastern Gulf Coast. This taxon is known to range up into the middle part of the Lisbon Formation (Middle Eocene Claiborne Group) (Frederiksen, 1988).

Lanagiopollis cribellata (Srivastava 1972) Frederiksen 1988

Plate 10, figures 9-10

Tricolporopollenites kruschii (Potonié 1934) Thomson & Pflug 1953. Elsik, 1968b, p.628, pl. 31, figs. 11, 13-15 only; pl. 32, figs. 1-3, 7 only.

Margocolporites cribellatus Srivastava, 1972, p. 260, 262, 264; pl. 19, figs. 1-8; pl. 20, figs. 1-2.

Lanagiopollis cribellata (Srivastava) Frederiksen, 1988, p. 56, pl. 11, fig. 17; Jardine and Harrington, 2008, pl. 3, fig. 13.

Dimensions. Polar diameter 33 μm (one specimen measured); equatorial diameter 33 – 39 μm , mean 37 μm (three specimens measured). Srivastava (1972) gave a range of 20 – 38 μm for the protologue specimens.

Remarks. *Lanagiopollis cribellata* has long colpi that extend $\sim 2/3$ the distance to the poles, and are bordered by nexinal thickenings 1-2 μm wide. The amb is obtuse-convex-triangular and the grain is oblate. Rare equatorial views (Plate 10, figure 9) demonstrate that the ora are lalongate and conspicuous. The sexine is microreticulate to punctate and homobrochate, with lumina/punctae $\sim 0.5 \mu\text{m}$ wide. *Lanagiopollis crassa* includes grains with a similar ornamentation to *Lanagiopollis cribellata*, but differs in having a thicker exine and lacking thickened margins. Other *Lanagiopollis* types from the Gulf Coast have a coarser ornamentation. *Lanagiopollis lihoka* and *Lanagiopollis hadrodictya* also differ in being heterobrochate, with larger lumina on the mesocolpia than on the apocolpia and at the colpi margins. *Nyssapollenites explanata* (Anderson 1960) Pocknall & Nichols 1996 has poorly defined ora, unbordered colpi, and has a punctate, intrarugulate sculpture.

Botanical affinity. Possibly *Alangium* (Frederiksen in Frederiksen et al., 1983; Frederiksen, 1988).

Occurrence. Occurred in relative abundances of <4% in 54/151 samples, from the Naheola to the Tusahoma formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Lanagiopollis eocaenica type of Frederiksen 1988

Plate 10, figures 11-12

Lanagiopollis eocaenica type. Frederiksen, 1988, p. 56-57, pl. 12, figs. 9-10; pl. 13, figs. 1-3.

Dimensions. Polar diameter 26 – 29 μm (two specimens measured); equatorial diameter 25 – 38 μm , mean 31 μm (three specimens measured). Krutzsch (1969) gave a range of 20 – 50 μm for the polar diameter of the protologue specimens, and a range of 35 – 45 μm for the equatorial diameter.

Remarks. This taxon includes oblate to prolate spheroidal pollen with a muri-clavate reticulate exine. The colpi are up to 2/3 the length of the polar axis, and only lightly bordered by thickenings. The ora are lalongate. The exine is 2 – 3.5 μm thick, the lumina are 1 – 2 μm wide, and the muri are 0.5 – 1 μm wide. Frederiksen (1988) referred his Gulf Coast specimens to *Lanagiopollis eocaenica* type, because the muri were dupli- to polybaculate, whereas in Krutzsch's (1969) original sketch they are simplibaculate (Frederiksen, 1988). My specimens are mainly dupli- to polybaculate, and so I have followed Frederiksen (1988) in assigning my specimens to his *Lanagiopollis eocaenica* type, rather than to the species itself. *Lanagiopollis hadrodictya* has a coarser reticulum; *Lanagiopollis lihoka* has more distinctly thickened margins, a thinner exine, and a heterobrochate reticulum.

Botanical affinity. Possibly *Alangium* (Frederiksen in Frederiksen et al., 1983; Frederiksen, 1988).

Occurrence. Occurred in relative abundances of <4% in 8/151 samples, in the Tallahatta and Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the middle part of the Lisbon Formation (Middle Eocene Claiborne Group) (Frederiksen, 1988).

Lanagiopollis hadrodictya Frederiksen 1988

Plate 10, figures 13-14

Alangipollis sp. Frederiksen, 1980a, p. 58, pl. 14, figs. 7-8.

Lanagiopollis hadrodictya Frederiksen, 1988, p. 57, pl. 13, figs. 4-12.

Dimensions. Polar diameter 31 – 32 μm (two specimens measured); equatorial diameter 26 – 40 μm , mean 32 μm (four specimens measured). Frederiksen (1988) gave a range of 33 – 42 μm for the equatorial diameter of the protologue specimens.

Remarks. *Lanagiopollis hadrodictya* has more deeply incised colpi than other species of

Lanagiopollis found on the US Gulf Coast, leading to a more lobate amb. The grain is spheroidal to oblate spheroidal in equatorial view. The colpi extend 1/2 to 3/4 of the way to the pole, and thickened margins may be distinct or indistinct. The exine is typically 3 – 4 μm thick. The sexine is coarsely muri-clavate reticulate, with polygonal lumina 1.5 – 2.5 μm wide. The muri are 1 – 1.5 μm wide and simplibaculate to duplibaculate. Like *Lanagiopollis lihoka* the reticulum is heterobrochate with wider lumina on the mesocolpia, although this is less pronounced in *Lanagiopollis hadrodictya*. *Lanagiopollis lihoka* also has a thinner exine and less angular lumina. *Lanagiopollis eocaenica* has a finer reticulum, and *Rhoipites capax* is more prolate, has a coarser reticulum, and more distinct margins.

Botanical affinity. Frederiksen (1980a) suggested Cornaceae, and probably *Alangium*.

Occurrence. Occurred in relative abundances of <3% in 6/151 samples, in the Tallahatta Formation on the eastern Gulf Coast. Rare specimens have been recorded as high as the Late Eocene Jackson Group (Frederiksen, 1980a), although these may be reworked (Frederiksen, 1988).

Lanagiopollis lihoka (Srivastava 1972) Frederiksen 1988

Plate 10, figure 15

Tricolporopollenites kruschii (Potonié 1934) Thomson & Pflug 1953. Elsik, 1968b, p.628, pl. 32, figs. 4-5 only; pl. 33, figs. 1-3, 8 only.

Margocolporites lihokus Srivastava, 1972, p. 264, pl. 20, figs. 3-5.

Lanagiopollis lihoka (Srivastava) Frederiksen, 1988, p. 56; Jardine and Harrington, 2008, pl. 3, fig. 14.

Dimensions. Polar diameter 36 μm (one specimen measured); equatorial diameter 32 – 44 μm , mean 39 μm (three specimens measured). Srivastava (1972) gave a range of 34 – 45 μm for the protologue specimens.

Remarks. This taxon is distinguished by its heterobrochate reticulum, which has lumina $<1 - 3\ \mu\text{m}$ wide on the mesocolpia, and $<0.5 - 1\ \mu\text{m}$ wide on the apocolpia and near the colpi margins. The amb is obtuse-convex-triangular. The colpi extend $\sim 3/4$ the way to the poles, and are bordered by thickenings $2-3\ \mu\text{m}$ wide. As with *Lanagiopollis cribellata*, the ora are lalongate. The exine is $\sim 2\ \mu\text{m}$ thick at the mesocolpia, and thins slightly towards the colpi. *Lanagiopollis cribellata* and *Lanagiopollis eocaenica* both have homobrochate reticula, and *Lanagiopollis hadrodictya* has a generally coarser reticulum and a thicker exine.

Botanical affinity. Possibly *Alangium* (Frederiksen in Frederiksen et al., 1983; Frederiksen, 1988).

Occurrence. Occurred in relative abundances of $<7\%$ in 36/151 samples, from the Naheola to the Tusahoma formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Nuxpollenites* Elsik 1974 emend. Frederiksen 1980

Type species. *Nuxpollenites claibornensis* Elsik 1974.

Remarks. This genus is distinguished by its thickened exine at the poles, which is caused by a distinctly columellate endosexine that is only present at the polar regions, and wedges out away from the poles. The grains are prolate and are either psilate all over, or ornamented by grana or verrucae in the equatorial region.

Nuxpollenites crockettensis Elsik 1974

Plate 10, figure 19

Nuxpollenites crockettensis Elsik, 1974, p. 100, pl. 4, figs. 141-146; Frederiksen, 1980b, p. 165, pl. 2, fig. 25-26.

Dimensions. Polar diameter 28 μm ; equatorial diameter 16 μm (one specimen measured). Elsik (1974a) gave a range of 23 – 35 μm for the polar diameter of the protologue specimens, and a range of 12 – 13 μm for the equatorial diameter.

Remarks. *Nuxpollenites crockettensis* has sculptural elements (grana or verrucae) about the meridonal zone of the grain surface. The exine is 3 – 4 μm thick at the poles and 1.5 – 2 μm thick at the equator. The colpi almost reach the poles and are unbordered, and the ora are indistinct and lalongate. The exine on my specimen is 3 μm thick at the poles and 2 μm thick at the equator; the difference in thickness is therefore not as extreme as on some specimens, but still within the range given by Elsik (1974a). The sculpture comprises verrucae <2 μm wide. *Nuxpollenites psilatus* is psilate to indistinctly punctate over the whole grain surface; *Nuxpollenites claibornensis* Elsik 1974 has a wider zone of meridonal sculpture and more rounded poles in equatorial view.

Botanical affinity. Unknown.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast. This taxon is known to range up into the middle of the Claiborne Group (Elsik, 1974a).

Nuxpollenites psilatus Frederiksen 1979

Plate 10, figure 20

Nuxpollenites sp. Elsik, 1974, pl. 4, figs. 126-127 only.

Nuxpollenites psilatus Frederiksen, 1979, p. 161, pl. 4, figs. 21-23; Frederiksen, 1980b, pl. 2, figs. 27-29.

Dimensions. Polar diameter 26 – 28 μm ; equatorial diameter 14 μm (two specimens measured). Frederiksen (1979) gave a range of 25 – 34 μm for the polar diameter of

the protologue specimens.

Remarks. This species lacks any sculpturing in the equatorial region, and is psilate to indistinctly punctate over the entire grain surface. The grain is prolate to perprolate in shape with straight sides. The colpi are slit-like and unbordered, and the ora are distinct and lalongate. *Nuxpollenites psilatus* differs from other species in this genus by its lack of a meridional sculpture.

Botanical affinity. Unknown.

Occurrence. Three specimens recorded in the Hatchetigbee Formation on the eastern Gulf Coast. This taxon is known to range up into the lower part of the Claiborne Group on the Gulf Coast (Frederiksen, 1979).

Genus *Nyssa* Linnaeus

Remarks. Pollen of extant *Nyssa* is oblate to suboblate in shape with distinct, endannulate, circular ora, long, narrow colpi, and an infrapunctate exine.

Nyssapollenites accommodates similar pollen that cannot be assigned confidently to the extant genus.

Nyssa kruschii group

Plate 10, figures 21-23

Pollenites kruschi Potonié, 1931b, p. 4, fig. 11

Tricolporopollenites kruschii (Potonié) Thomson and Pflug, 1953, p. 103, pl. 13, fig. 14-63; Elsik, 1968b, pl. 34, figs. 3a-b only.

Nyssa kruschii (Potonié) Frederiksen, 1980a, p. 54-55, pl. 13, fig. 1; Harrington, 2003b, pl. 1, fig. 28.

Rhoipites angustus Frederiksen, 1980a, p. 55, pl. 13, fig. 2-8.

"*Tricolporopollenites dolium*" of Engelhardt 1964. Frederiksen, 1980b, p. 166, pl. 4, fig. 25.

Nyssa sp. Frederiksen, 1980b, p. 166, pl. 4, fig. 28.

Nyssapollenites kruschii Jardine and Harrington, 2008, pl. 3, fig. 15.

Dimensions. Polar diameter 18 – 33 μm , mean 26 μm (10 specimens measured); equatorial diameter 16 – 29 μm , mean 22 μm (14 specimens measured). Potonié (1931b) gave a range of 28 – 32 μm for the equatorial diameter of *Pollenites kruschi*. Frederiksen (1980a) gave a range of 24 – 35 μm for the polar diameter of *Rhoipites angustus*.

Remarks. This group includes *Nyssa kruschii* and *Rhoipites angustus*. Both possess an infrapunctate to minutely microreticulate exine, long, narrow colpi and small, round ora, but differ in their overall shape: *Nyssa kruschii* is oblate to suboblate, and *Rhoipites angustus* is prolate to prolate spheroidal. *Nyssa kruschii* is also endannulate, whereas *Rhoipites angustus* is not. However, these two species appear to form the end members of a morphological continuum that was not always easy to divide consistently. Both prolate and oblate forms are also long ranging and of little stratigraphic value within the current time frame, and so I have counted them together as one group.

Botanical affinity. At least in part *Nyssa* (Frederiksen, 1980a), although the lack of an endannulus in *Rhoipites angustus* types does cast some doubt upon the affinity of these specimens. Frederiksen (1980a) also likened *Rhoipites angustus* to *Mastixia* (Cornaceae) and *Rhus* (Anacardiaceae).

Occurrence. Occurred in relative abundances of <11% in 119/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This group is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Genus *Nyssapollenites* Thiergart 1938 ex Potonié 1960

Type species. *Nyssapollenites pseudocruciatus* (Potonié 1931) Thiergart 1938.

Remarks. This form genus includes nysoid-type pollen (i.e. spherical to oblate, tricolporate pollen with endannulate ora and long, narrow colpi, and an infrapunctate exine) that cannot be assigned confidently to *Nyssa*. *Rhoipites* comprises prolate pollen that is typically more coarsely reticulate, *Lanagiopollis* is reticulate or rugulate, and *Siltaria* is scabrate and has lalongate ora.

Nyssapollenites paleocenicus Frederiksen 1980

Plate 11, figure 1

Nyssapollenites paleocenicus Frederiksen, 1980b, p. 166, pl. 3, figs. 6-12.

Dimensions. Equatorial diameter 23 μm (one specimen measured). Frederiksen (1980b) gave a range of 16 – 22 μm for the equatorial diameter of the protologue specimens.

Remarks. *Nyssapollenites paleocenicus* is oblate to spheroidal and has a thick nexine and a distinctly columellate, punctate sexine. The exine is typically 1.5 – 2 μm thick in the intercolpia and may be thicker; it thins to ~1 μm at the colpi. The single specimen in my material has an exine 2 μm thick in the intercolpia. The sexine:nexine ratio is ~1:1. The colpi are unbordered and the ora are indistinct and lack endannuli.

Botanical affinity. Unknown. The lack of endannuli suggests that this species does not represent *Nyssa*.

Occurrence. One specimen recorded from the Porters Creek Formation on the eastern Gulf Coast. This species is very abundant in the lowermost Paleocene of South Carolina (Frederiksen, 1980b), and so may increase in abundance in the lower Porters Creek and Clayton formations.

Nyssapollenites pulvinus (Potonié 1931) Frederiksen 1980

Plate 11, figure 2

Pollenites pulvinus Potonié, 1931b, p. 4, fig. 23.

Nyssapollenites pulvinus (Potonié) Frederiksen, 1980a, p. 55, pl. 12, fig. 28-29.

Dimensions. Equatorial diameter ~29 μm (one specimen measured; grain orientated at an oblique and angle and deformed). Potonié (1931b) gave a range of 21 – 30 μm for the equatorial diameter of the protologue specimens.

Remarks. This species represents oblate to spheroidal pollen with a triangular to circular amb, distinct circular pores and colpi bordered by thickened margins. Although Potonié's (1931b) original description stated that this species is granulate, his illustration is distinctly punctate/microreticulate, as is the specimen illustrated by Frederiksen (1980a). Other species in this genus typically have a finer ornamentation. *Lanagiopollis* spp. are generally larger and have wider colpi and ora.

Botanical affinity. Frederiksen (1980a) suggested Nyssaceae or Cornaceae.

Occurrence. One specimen recorded in the Hatchetigbee Formation on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Nyssapollenites spp.

Plate 11, figures 3-5

Dimensions. Polar diameter 22 – 36 μm , mean 29 μm (five specimens measured); equatorial diameter 16 – 28 μm , mean 24 μm (eight specimens measured).

Remarks. This taxon includes nysoid pollen that does not fit comfortably into any existing species. The grain is oblate to subprolate and in polar view the amb is convex-triangular to sub-circular. The exine is infrapunctate. This generalised

group is heterogeneous in terms of size, exine thickness and colpi and pore style, but specimens did not vary systematically enough to consistently divide them into more closely circumscribed species. “Cf. *Symplocoipollenites*” Elsik 1968 is similar to some specimens but has fine nexinal striations and shorter colpi.

Botanical affinity. Unknown. All specimens depart from the *Nyssa* morphological type and so an affinity with *Nyssa* is unlikely. An affinity with Nyssaceae is not precluded.

Occurrence. Occurred in relative abundances of <8% in 102/151 samples, from the Porters Creek to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Porocolpopollenites* Pflug in Thomson & Pflug 1953

Remarks. See Chapter 4 for genus remarks and type species.

Porocolpopollenites ollivierae (Gruas-Cavagnetto 1976) Frederiksen in Frederiksen et al.
1983

Plate 11, figures 6-8

Intratrisporopollenites ollivierae Gruas-Cavagnetto, 1976, p. 31, pl. 4, fig. 2-4, 6-8, 10;
Frederiksen, 1980b, p. 168, 170, pl. 3, fig. 26-27.

Riestedtipollis? sp. Frederiksen, 1979, p. 160, pl. 4, fig. 7-10.

Porocolpopollenites ollivierae (Gruas-Cavagnetto) Frederiksen in Frederiksen et al.,
1983, p. 65-66, pl. 18, fig. 26-28; Harrington, 2003b, pl. 1, figs. 30-31.

Dimensions. Equatorial diameter 20 – 30 μm , mean 26 μm (nine specimens measured). Gruas-Cavagnetto (1976) gave a range of 22 – 32 μm for the protologue

specimens.

Remarks. This taxon represents tri- and tetracolporate pollen grains that are suboblate to spheroidal in shape and have a convex-triangular to convex-square to circular amb. This species is variable in terms of exine thickness, sexine:nexine ratio and sculpture. As with Frederiksen's (in Frederiksen et al., 1983) specimens from San Diego grains in my material were variously microreticulate, granulate or verrucate, although the grains were often corroded and surface details were hard to determine. Nexinal cracks are present in some specimens (e.g. Plate 11, figure 6) and appear to be a diagnostic feature of this species (Frederiksen in Frederiksen et al., 1983). The sexine is columellate. The colpi are short, boat-shaped and lightly bordered by sexinal thickenings. The ora are lalongate and bordered above and below (i.e. on their polar sides) by endannuli up to 3 μm thick. The ends of the ora are unbordered and indistinct. A (post)vestibulum is always present. The few specimens recovered from the Paleocene were tricolporate; tetracolporate forms first appear in the Hatchetigbee Formation, and in the Tallahatta Formation are dominant. This supports the general evolutionary pattern described by Frederiksen (in Frederiksen et al., 1983) for this lineage. *Tricolpites redactus* Frederiksen 1978 is similar but is tricolpate and lacks an endannulus. All specimens assigned to *Symplocos?* are exclusively tri-aperturate and lack nexinal striations.

Botanical affinity. Frederiksen (in Frederiksen et al., 1983) listed a number of morphological similarities with certain species of *Symplocos*, and also listed Apocynaceae, Melliaceae, Styracaceae, and Verbenaceae as possible parent families.

Occurrence. Occurred in relative abundances of <6% in 20/151 samples, from the Nanafalia to the Tallahatta formations on the eastern Gulf Coast. This taxon is rare in the Paleocene, and increases in abundance in the Eocene.

Genus *Rhoipites* Wodehouse 1933

Remarks. See Chapter 4 for genus remarks and type species.

Rhoipites bradleyi Wodehouse 1933

Plate 11, figure 14

Rhoipites bradleyi Wodehouse, 1933, p. 513, fig. 45; Nichols, 2010, p. 70, pl. 17, figs. 1-4.

Dimensions. Polar diameter 31 – 34 μm , mean 33 μm ; equatorial diameter 22 – 25 μm , mean 23 μm (three specimens measured). Specimens of *Rhoipites bradleyi* in Wodehouse's (1933) original material have a polar diameter of 35 μm , and an equatorial diameter of 24 – 30 μm (Nichols, 2010).

Remarks. This species is characterised by its fine reticulum with lumina of 0.5 – 1 μm in diameter, and its well-developed costae colpi that flare out at the pores. The grain shape can vary from spheroidal to prolate. The examples of this taxon in my material match well with the redescription and illustrations of Wodehouse's (1933) original specimens provided by Nichols (2010). *Rhoipites cryptoporus* is similar in many respects, but differs in having a coarser reticulum (lumina 0.5 – 2 μm in diameter) and circular, endannulate ora.

Affinity. Unknown.

Occurrence. Three specimens recorded in the Nanafalia and Tuscaloosa formations on the eastern US Gulf Coast. This taxon was only found in samples from the Red Hills Mine in Mississippi.

Rhoipites capax Frederiksen 1988

Plate 11, figures 15-16

Rhoipites capax Frederiksen, 1988, p. 54, pl. 13, figs. 13-14; pl. 14, figs. 1-7.

Dimensions. Polar diameter 36 μm ; equatorial diameter 31 μm (one specimen measured). Frederiksen (1988) gave a range of 37 – 52 μm for the polar diameter of the protologue specimens.

Remarks. *Rhoipites capax* is very coarsely reticulate, with lumina 3 – 4 μm in diameter and muri 0.6 – 1.5 μm wide. The muri are simpli- to duplibaculate and the columellae appear almost gemmate in optical section. The colpi extend nearly the full length of the grain and are bordered by strips of granulate sexine, and distinct thickenings of the nexine (costa) that are 2 – 4 μm wide at the equator and narrow towards the poles. The ora are round to lalongate and up to 6 – 7.5 μm in diameter, and bordered by indistinct endannuli 2 – 3 μm wide. The grain is spheroidal to subprolate.

Rhoipites cryptoporus and *Rhoipites latus* are both more prolate and have finer reticula, *Lanagiopollis* spp. all have finer reticula and are typically more oblate, and *Rousea monilifera* Frederiksen 1980 is tricolpate and has exclusively simplibaculate muri.

Botanical affinity. Unknown.

Occurrence. Two specimens recorded in the Zilpha Formation on the eastern Gulf Coast. This taxon is known to range down into the Tallahatta Formation, and up into the top part of the Lisbon Formation (Frederiksen, 1988).

Rhoipites cryptoporus Srivastava 1972

Plate 11, figure 17

Rhoipites cryptoporus Srivastava, 1972, p. 270, pl. 21, fig. 1 – 11; Jardine and Harrington, 2008, pl. 3, fig. 19.

cf. *Tricolporopollenites explanata* (Anderson 1960) Elsik, 1968b, p. 628, pl. 33, fig. 6 only.

Dimensions. Polar diameter 25 – 37 μm , mean 32 μm ; equatorial diameter 20 – 26 μm , mean 23 μm (10 specimens measured). Srivastava (1972) gave a range of 27 – 36 μm for the polar diameter of the protologue specimens, and a range of 18 – 27 μm for the equatorial diameter.

Remarks. This species is prolate and muri-clavate reticulate, with lumina 0.5 – 2 μm in diameter and muri \sim 1 μm wide. The reticulum is heterobrochate, with larger lumina on the mesocolpia and fining towards the colpi. The colpi are long and bordered by thickened margins. The endopores are circular and 2 – 3 μm wide, and bordered by indistinct endannuli $<$ 1 μm wide. *Rhoipites bradleyi* Wodehouse 1933 is similar but has a finer, homobrochate reticulum with relatively thinner muri. *Rhoipites latus* has polygonal to longitudinally elongate lumina that are up to 2.5 μm in greatest dimension. *Rhoipites* sp. 1 has larger and distinctly lolongate ora.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of $<7\%$ in 73/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Rhoipites latus Frederiksen 1980

Plate 11, figures 18-19

Tricolporopollenites sp 4. Engelhardt, 1964, p. 74, pl. 3, fig. 29.

Tricolporopollenites sp. Tschudy and Van Loenen, 1970, pl. 4, figs. 13a-b.

Tricolporites sp. Tschudy and Van Loenen, 1970, pl. 5, fig. 1.

Tricolporopollenites. n. sp. B (*Parthenocissus* type). Tschudy, 1973a, p. B17, pl. 4, figs. 18-19.

Rhoipites latus Frederiksen, 1980a, p. 55-56, pl. 13, fig. 9-13.

Dimensions. Polar diameter 32 μm ; equatorial diameter 22 μm (two specimens

measured). Frederiksen (1980a) gave a range of 34 – 44 μm for the polar diameter of the protologue specimens.

Remarks. This species is characterised by its prolate shape, and reticulum that is formed of polygonal to longitudinally elongate lumina and relatively thick muri. The lumina measure 0.5 – 1.5 μm x 1 – 2.5 μm , and the muri are 0.5 – 0.8 μm wide, duplibaculate and clavate in optical section. The exine is ~2 μm thick. The colpi are narrow and extend almost the full length of the grain, and are bordered by thickenings 1.5 – 2 μm wide. The ora are distinct and \pm circular; they measure 2.5 – 3.5 μm in diameter. *Horniella brevicolpata* also has lumina that are longitudinally elongate, but the grain is larger, the exine is thinner and the colpi are relatively shorter, unbordered and less distinct. *Rhoipites cryptoporus* has larger but less distinct ora, the lumina are not longitudinally elongated, and the grain is prolate to prolate spheroidal.

Botanical affinity. Similar to pollen of *Parthenocissus* (Vitaceae) (Tschudy and van Loenen, 1970; Tschudy, 1973a).

Occurrence. Occurred in relative abundances of <1.4% in 4/151 samples, in the Tallahatta and Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Genus *Siltaria* Traverse 1955

Type species. *Siltaria scabriextima* Traverse 1955.

Remarks. This genus includes pollen grains that are distinctly columellate, and have a very fine scabrate sculpture, long colpi, and large, elliptical to elongate ora. *Nyssapollenites* has round ora, an infrapunctate exine and is oblate; *Horniella*, *Rhoipites* and *Caprifoliipites* are all reticulate.

"Siltaria cf. S. scabriextima" of Frederiksen 1980

Plate 12, figures 8-11

Siltaria cf. S. scabriextima Traverse 1955. Frederiksen, 1980a, p. 52, pl. 11, figs. 26-28; Jardine and Harrington, 2008, pl. 3, fig. 25.

Dimensions. Polar diameter 13 – 23 μm , mean 19 μm ; equatorial diameter 11 – 16 μm , mean 14 μm (six specimens measured). Frederiksen (1980a) provided a polar diameter of under 25 μm for his specimens.

Remarks. *Siltaria scabriextima* Traverse 1955 is prolate to subprolate, has distinct lalongate ora, a columellate, scabrate exine, and is ~32 μm in polar diameter. The colpi and ora are lightly bordered. Frederiksen (1980a) referred otherwise similar specimens that were 25 μm or less in polar diameter to *Siltaria cf. S. scabriextima*. My specimens are similar in size or perhaps smaller than Frederiksen's (1980a) but otherwise conform to the description of *Siltaria scabriextima* given by Traverse (1955), and so I have used Frederiksen's (1980a) informal designation. In some specimens the ora are sufficiently meridionally elongate to meet at the ends. *Cupuliferoipollenites* spp. has a smooth exine, is not columellate, and has more or less round rather than elliptical ora. The *Siltaria-Cyrillaceaepollenites* complex includes columellate, scabrate forms but these are more spheroidal in shape and have \pm geniculate colpi. *Siltaria hanleyi* Pocknall & Nichols 1996 is more distinctly prolate and has less lalongate ora.

Botanical affinity. Frederiksen (1980a) suggested *Rhus* (Anacardiaceae) as a possible affinity.

Occurrence. Occurred in relative abundances of <2.1% in 17/151 samples, from the Naheola to the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Siltaria-Cyrillaceaepollenites Complex

Plate 12, figures 12-15

Siltaria pacata (Pflug in Thomson & Pflug 1953) Frederiksen, 1980a, p. 52, pl. 11, fig. 25.

Cyrillaceaepollenites kedvesii Frederiksen, 1980a, p. 51, pl. 11, fig. 13-18.

Cyrillaceaepollenites sp. Frederiksen, 1980b, p. 164, pl. 4, fig. 27.

Cyrillaceaepollenites megaexactus (Potonié 1931) Potonié 1960. Frederiksen, 1980a, p. 51, pl. 11, figs. 19-22; Frederiksen, 1980b, p. 164.

Cyrillaceaepollenites cf. *C. megaexactus* Tschudy, 1973a, p. B17, pl. 4, fig. 14-17.

Siltaria abouziarovae group. Frederiksen, 1988, p. 54, pl. 8, fig. 19-22.

Dimensions. Polar diameter 13 – 29 μm , mean 20 μm ; equatorial diameter 16 – 28 μm , mean 20 μm (13 specimens measured).

Remarks. On the Gulf Coast spheroidal, tricolporate pollen with more or less geniculate colpi and lalongate ora occurs as both *Siltaria* (columellate and scabrate/punctate exine) and *Cyrillaceaepollenites* (lacking columellae and psilate exine) types. Frederiksen (1988) grouped together *Siltaria abouziarovae* (referred to as *Siltaria pacata* in Frederiksen (1980a)) and *Cyrillaceaepollenites kedvesii* because they are similar in size (18 – 28 μm) and overall appearance, and therefore difficult to distinguish consistently under routine light microscopy. To this group I have added *Cyrillaceaepollenites megaexactus*, which is smaller (14 – 22 μm) and has a variable aperture structure, and similar sized grains possessing columellae that would be referable to *Siltaria* but do not correspond to an existing taxon. Although these morphotypes are smaller there did not appear to be two distinct size-based groups within my material, and for the sake of consistent taxonomy I have counted them all together.

Botanical affinity. In part probably Cyrillaceae; specimens corresponding to *Siltaria*

abouziarovae may represent *Diospyros* (Ebenaceae) (Frederiksen, 1980a).

Occurrence. Occurred in relative abundances of <9% in 95/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. Similar forms range up into the Early Oligocene Vicksburg Group (Frederiksen, 1988).

Genus *Spinaepollis* Krutzsch 1961

Type species. *Spinaepollis spinosus* (Potonié 1931) Krutzsch 1961

Remarks. This genus includes oblate to oblate spheroidal, tricolporate pollen with a subcircular amb and a dense, echinate ornamentation. The echinae are arranged into rosettes over the grain surface. The apertures are typically obscured by the exine ornamentation. *Sernapollenites* Stover in Stover et al 1966 is a junior synonym of this genus.

Spinaepollis spinosa (Potonié 1931) Krutzsch 1961

Plate 12, figure 16

Pollenites spinosus Potonié, 1931a, p. 328, pl. 1, figs. 29-32.

Spinaepollis spinosus (Potonié) Krutzsch, 1961, p. 323; Tschudy, 1973a, p. B12, pl. 1, figs. 10-12; Frederiksen, 1979, p. 139; Jardine and Harrington, 2008, pl. 3, fig. 26.

Sernapollenites duratus Stover in Stover et al., 1966, p. 3-4, pl. 1, figs. 7-8; Elsik, 1968b, p. 618-620, pl. 21, figs. 7-8; Fairchild and Elsik, 1969, p. 85, pl. 38, fig. 41.

Dimensions. Equatorial diameter 24 – 25 μm (two specimens measured). Potonié (1931a) gave an equatorial diameter of $\sim 30 \mu\text{m}$ for the protologue specimens. Stover (in Stover et al., 1966) gave a range of 28 – 35 μm for the equatorial diameter of

Sernapollenites duratus.

Remarks. The main morphological features of this species have been described in the genus remarks. The echinae on my specimens are 1.5 – 2.5 μm in length.

Malvacipollis spp. lacks colpi and has smaller and more sparsely distributed echinae.

Compositoipollenites also lacks colpi and has larger, more thorn-like spines that are not arranged in rosettes.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <8% in 73/151 samples, from the Naheola to the lowermost Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Symplocoipollenites* Potonié 1951 ex Potonié 1960

Type species. *Symplocoipollenites vestibulum* (Potonié 1931) Potonié 1951 ex Potonié 1960

Remarks. This genus includes oblate pollen grains with a triangular amb, which are brevicolpate, vestibulate, and have a granulate to rugulate exine. *Symplocoipollenites* is therefore similar to *Porocolpopollenites* but is more closely circumscribed in terms of the amb shape and exine sculpture.

“cf. *Symplocoipollenites* sp.” of Elsik 1968

Plate 12, figures 17-22

cf. *Symplocoipollenites* sp. Elsik, 1968b, p. 636, pl. 29, figs. 3-6; Jardine and Harrington, 2008, pl. 3, fig. 27.

Rhoipites sp. 3. Jardine and Harrington, 2008, pl. 3, fig. 22.

Dimensions. Equatorial diameter 31 – 41 μm , mean 33 μm (18 specimens measured).

Remarks. This species includes oblate pollen grains with a convex-triangular to subcircular amb. The colpi extend about half the distance to the poles, are narrow and shallow, and may be lightly bordered by thickenings 1 – 2 μm wide. The ora are vestibulate, and in equatorial view are lalongate and slit-like, and 0.5 – 1 μm high by 5 – 6 μm wide. The ora are bordered above and below by thickenings, and the sides are bordered by thinned exine 0.5 – 1.5 μm wide, which may continue polewards alongside the colpi margins (see Plate 12, figures 18, 19 and 21). The exine is typically 1 – 2 μm thick in the intercolpial areas, with a sexine:nexine ration of 2:1. Towards the apertures the nexine thickens so that the exine is 2 – 3 μm thick. The sexine is distinctly columellate and minutely microreticulate to punctate. The nexine is often marked by very fine, irregular striations that may run parallel to the amb or may be more irregular.

This taxon intergrades with *Nyssapollenites* on one hand and *Holkopollenites* on the other. It differs from *Nyssapollenites* in having distinctly lalongate ora and margins that do not extend the whole length of the grain. It differs from *Holkopollenites* in being less sharply punctate, having much less deeply incised colpi, a convex-triangular rather than deltoid amb, and much finer nexinal striations. Some specimens were documented that appear to be midway between *Holkopollenites chemardensis* and cf. *Symplocoipollenites* sp. (e.g. Plate 9, figure 19, and plate 12, figure 18).

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <33% in 70/151 samples, from the Porters Creek to the lowermost Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

Genus *Symplocos* Jacquin

Remarks. See Chapter 4 for genus remarks.

Symplocos? contracta Frederiksen 1980

Plate 12, figures 23-24

Symplocoipollenites sp. 1. Enghardt, 1964, p. 75, pl. 4, fig. 39.

Triporopollenites sp. Tschudy and Van Loenen, 1970, pl. 3, fig. 13.

Porocolpopollenites spp. (psilate-microreticulate) Tschudy, 1973a, p. B15, pl. 3, figs. 5-6.

Symplocos contracta Frederiksen, 1980a, p. 61, pl. 15, figs. 6-9; Harrington, 2003b, pl. 1, fig. 6.

Dimensions. Equatorial diameter 23 – 28 μm (two specimens measured). Frederiksen (1980a) gave a range of 22 – 34 μm for the protologue specimens.

Remarks. This species is peroblate with a straight-triangular to slightly convex-triangular amb, a punctate exine and sexine that thins towards the apertures. The colpi are 1 – 2.5 μm long and unbordered, the ora are obscure with slit-like vestibula <0.5 μm deep. *Symplocos? virginensis* differs in being atriate and microreticulate rather than vestibulate and punctate. Frederiksen (1988) considered these two morphotypes to be too similar to consistently tell apart, and counted them together as one generalised group. However, as *Symplocos? contracta* is an Eocene marker taxon on the US Gulf Coast (Harrington, 2003), and *Symplocos? virginensis* is present in the Late Paleocene strata, it is worthwhile maintaining the distinction. Other species of *Symplocos?* differ in either lacking sexine that thins towards the apertures, in having concave sides, or in their exine ornamentation.

Botanical affinity. Probably *Symplocos* (Symplocaceae) (Frederiksen, 1980a).

Occurrence. Two specimens recorded from the Tallahatta Formation on the eastern

Gulf Coast. This taxon is known to range from the uppermost (Eocene) Tusahoma Formation (Harrington, 2003) to the Early Oligocene Vicksburg Group (Frederiksen, 1980a).

Symplocos? gemmata Frederiksen 1980

Plate 12, figure 25

Symplocoipollenites sp. Tschudy and Van Loenen, 1970, pl. 5, figs. 6a-b.

Porocolpopollenites spp. (verrucate) Tschudy, 1973a, p. B16, pl. 4, fig. 8-9.

Symplocos gemmata Frederiksen, 1980a, p. 61-62, pl. 15, fig. 10-14.

Dimensions. Equatorial diameter 25 μm (one specimen measured). Frederiksen (1980a) gave a range of 19 – 31 μm for the protologue specimens.

Remarks. This species is characterised by its densely gemmate to granulate sculpture and straight-triangular to strongly convex-triangular amb. The gemmae are 0.3 – 1.5 μm in diameter and up to 1 μm high. The ora are vestibulate and endannulate; the endannuli are 2 – 3 μm thick. The colpi do not usually extend beyond the endannuli, and are 0.5 – 1 μm wide at the equator and narrow rapidly towards the poles. Other species of *Symplocos?* on the Gulf Coast are not gemmate. *Symplocos latiporis* (Pflug & Thomson) Frederiksen 1980 is more finely gemmate and has straight sides. *Symplocos calauensis* (Kruttsch, 1961) Frederiksen 1980 has a distinctly punctate exine between the gemmae.

Botanical affinity. Probably *Symplocos* (Symplocaceae) (Frederiksen, 1980a).

Occurrence. Three specimens recorded in the Tallahatta and Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the Late Eocene Yazoo Clay (Frederiksen, 1980a).

Symplocos? thalmanii (Anderson 1960) Frederiksen 1980

Plate 12, figures 26-27

Proteacidites thalmanii Anderson, 1960, p. 21, pl. 2, figs. 1-4; pl. 10, figs. 9-13.

Symplocos? thalmanii (Anderson) Frederiksen, 1980a, p. 62, pl. 15, fig. 21.

Dimensions. Equatorial diameter 26 μm (one specimen measured). Anderson (1960) gave a range of 17 – 29 μm for the protologue specimens.

Remarks. This species has a well-developed heterobrochate reticulum and thick endannuli. The lumina of the reticulum are 0.5 – 1 μm on the apocolpia and 1 – 2 μm on the mesocolpia. The endannuli are 2 μm deep, and the vestibula are ~1 μm deep. The colpi extend 1/3 – 1/2 the distance to the poles and are lightly bordered by thickenings. The amb is straight-triangular to weakly convex-triangular. Other species of *Symplocos?* on the Gulf Coast lack a coarse reticulum. *Proteacidites* sp. Pocknall and Nichols 1996 and *Proteacidites terrazus* Rouse 1962 may be conspecific with *Symplocos? thalmanii*, if further inspection reveals the apertures to be colporate rather than porate.

Botanical affinity. Probably *Symplocos* (Symplocaceae) (Frederiksen, 1980a).

Occurrence. Four specimens recorded in the Calvert Bluff Formation in Texas. This species is more common in the uppermost Cretaceous, and it is not clear if these Late Paleocene specimens, and those that Frederiksen (1980a) reported from the Middle Eocene of the eastern Gulf Coast, are reworked. Alternatively, the disjointed stratigraphic range of this morphotype may indicate a polyphyletic group of plant taxa that produced morphologically similar pollen throughout the Late Cretaceous and Palaeogene (Frederiksen, 1980a).

Symplocos? virginensis (Frederiksen 1979) Frederiksen 1988

Plate 13, figures 1-2

Porocolpopollenites virginienensis Frederiksen, 1979, p. 161, pl. 4, fig. 13-18.

Symplocos? virginienensis (Frederiksen) Frederiksen, 1988, p. 55.

Dimensions. Equatorial diameter 29 μm (one specimen measured). Frederiksen (1979) gave a range of 22 – 32 μm for the protologue specimens.

Remarks. *Symplocos? virginienensis* is distinctly micro-reticulate and has atria 8 – 12 μm wide and 2 – 4 μm deep. The amb is \pm straight-triangular. The colpi extend 4 μm or less towards the pole on each hemisphere, and are 1 – 2 μm wide at the equator. As with *Symplocos? contracta* the sexine thins towards the apertures, but *Symplocos? virginienensis* differs in being microreticulate and atriate rather than punctate and vestibulate (see further discussion under *Symplocos? contracta*). *Symplocos? vestibuliformis* (Pflug in Thomson & Pflug 1953) Frederiksen 1980 differs in being psilate.

Botanical affinity. Probably *Symplocos* (Symplocaceae) (Frederiksen, 1988).

Occurrence. One specimen recorded in the lowermost Tuscaloosa Formation of the eastern Gulf Coast (Red Hills Mine samples). This taxon is known to range up to the Early to Middle Eocene Tallahatta Formation (Frederiksen, 1979).

Genus *Tetracolporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Type species. *Tetracolporopollenites sapotoides* Pflug & Thomson in Thomson & Pflug 1953.

Remarks. This genus includes pollen grains similar to those produced by the extant Sapotaceae (see Erdtman, 1952, p. 397). The grains are prolate to subprolate and oval with flattened poles in equatorial view. There are three or four colporate apertures with distinct, lalongate, elliptical or oval pores. The exine is typically psilate or scabrate, and may have a faint infra-texture. *Siltaria* differs in having a distinctly columellate exine, being exclusively tricolporate, and not being oval to egg-shaped in

equatorial view. *Quadrupollenites* has indistinct ora, nexinal thickenings surrounding the colpi, and does not incorporate tricolporate forms.

Tetracolporopollenites megadolium (Potonié 1934) Frederiksen 1980

Long colpate form: Plate 13, figure 6

Short colpate form: Plate 13, figures 7-8

Pollenites megadolium Potonié, 1931a, p. 332, pl. 1, figs. 16, 25 ex Potonié, 1934, p. 89, pl. 5, figs. 4-5, 7; pl. 6, fig. 35.

Tricolporopollenites sp. 6. Engelhardt, 1964, p. 74, pl. 3, fig. 31.

Tricolporites sp. Tschudy and Van Loenen, 1970, pl. 5, fig. 5.

Tetracolporopollenites megadolium (Potonié) Frederiksen, 1980a, p. 63, pl. 16, fig. 5.

"Sapotaceoidapollenites" megadolium (Potonié) Frederiksen, 1980b, p. 171.

Tetracolporopollenites megadolium (short colpi). Frederiksen, 1988, p. 53, pl. 8, fig. 16.

Tetracolporopollenites megadolium (long colpi). Frederiksen, 1988, p. 53, pl. 8, figs. 17-18.

Dimensions. Polar diameter 27 – 35 μm , mean 33 μm ; equatorial diameter 21 – 25 μm , mean 22 μm (five specimens measured). Potonié (1931a) gave a range of 40 – 80 μm for the polar diameter of the protologue specimens. Frederiksen (1980a) gave a range of 27 – 54 μm for the polar diameter of specimens from the US Gulf Coast; most were between 29 and 36 μm .

Remarks. This species is tricolporate, subprolate, has a psilate to punctate exine, and has distinct, lalongate ora. Frederiksen (1988) documented long and short colpate forms of *Tetracolporopollenites megadolium*; the short colpate form is the tricolporate equivalent of *Tetracolporopollenites brevis*, and the long colpate form is the tricolporate equivalent of *Tetracolporopollenites lesquereuxianus*. I followed Frederiksen's (1988) division when making initial counts, but combined both long and short colpate forms of *Tetracolporopollenites megadolium* together with *Tetracolporopollenites brevis*

and *Tetracolporopollenites lesquereuxianus* for analytical purposes. It is plausible and even likely that all four morphotypes were produced by the same plant species (Frederiksen, 1980a), and combining the three- and four-aperturate types makes this taxon consistent with other zono-aperturate taxa that were not split-up based on aperture number (e.g. *Porocolpopollenites ollivierae* and *Intratrilporopollenites vespites*). *Tetracolporopollenites prolatus* is tricolporate but differs from *Tetracolporopollenites megadolium* in being smaller, prolate, and having bulging ora.

Botanical affinity. Sapotaceae (Frederiksen, 1980a).

Occurrence. Specimens with short colpi occurred in relative abundances of <3% in 7/151 samples, from the Hatchetigbee to the Zilpha formations on the eastern Gulf Coast. Specimens with long colpi occurred in relative abundances of <4% in 10/151 samples, from the Hatchetigbee to the Zilpha formations. Both types are known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1988).

Tetracolporopollenites prolatus Frederiksen 1988

Plate 13, figure 9

Tetracolporopollenites prolatus Frederiksen, 1988, p. 53, pl. 8, fig. 10-15.

Dimensions. Polar diameter 25 – 29 μm , mean 26 μm ; equatorial diameter 16 – 19 μm , mean 18 μm (three specimens measured). Frederiksen (1988) gave a range of 21 – 28 μm for the protologue specimens.

Remarks. This species is prolate in shape with straight sides except at the ora, which typically bulge outwards. The ora are also thickly endannulate. The colpi are narrow and long, and the exine is distinctly punctate. *Tetracolporopollenites prolatus* differs from other species in this genus by being smaller, more distinctly prolate, and in having bulging ora on most specimens.

Botanical affinity. Probably Sapotaceae.

Occurrence. Occurred in relative abundances of <8% in 5/151 samples, in the Tallahatta and Zilpha formations on the eastern Gulf Coast.

Genus *Tricolporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Remarks. See Chapter 4 for genus remarks and type species.

“Tricolporopollenites n. sp. A” of Tschudy 1973

Plate 13, figures 15-17

Tricolporopollenites n. sp. A (psilate, large pores) Tschudy, 1973a, p. B12, pl. 1, figs. 13-17.

Siltaria pacata (Pflug in Thomson & Pflug 1953) Frederiksen 1980. Jardine and Harrington, 2008 [misidentified], pl. 3, fig. 24.

Tricolporopollenites megadolium. Jardine and Harrington, 2008 [misidentified], pl. 3, fig. 28.

Dimensions. Polar diameter 29 – 40 μm , mean 33 μm ; equatorial diameter 23 – 38 μm , mean 30 μm (12 specimens measured).

Remarks. This species is typically prolate spheroidal in shape, although it varies from oblate spheroidal to prolate. It is characterised by its thick exine and large, distinct ora. The exine is 1.5 – 2 μm thick on well-preserved specimens. The sexine:nexine ratio is ~3:1, and the sexine is internally structureless and psilate, although on corroded specimens it may appear punctate or scabrate. The colpi are lightly bordered by thickenings and almost reach the poles. The ora are circular to lalongate, endannulate, and 4 – 10 μm in maximum dimension. *Tetracolporopollenites megadolium* has a thinner exine and more distinctly lalongate, ellipsoidal ora.

Tetracolporopollenites “binocularis” Jaramillo et al 2007 has thicker endannuli that extend up the sides of the colpi, and more distinctly lalongate ora, but is otherwise similar.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <4% in 28/151 samples, from the Naheola to the base of the Tallahatta formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

ZONOCOLPORATE POLLEN

Genus *Quadrapollenites* Stover in Stover et al. 1966

Type species. *Quadrapollenites vagus* Stover in Stover et al. 1966.

Remarks. *Quadrapollenites* includes prolate to prolate spheroidal tetracolporate pollen with psilate exine and indistinct ora. The colpi are costate except in the equatorial area. This genus differs from *Tetracolporopollenites* in having indistinct ora and a more rounded profile in equatorial view.

Quadrapollenites vagus Stover in Stover et al. 1966

Plate 13, figures 21-24

Quadrapollenites vagus Stover in Stover et al., 1966, p. 9, pl. 4, figs. 2-5; Elsik, 1968b, p. 630, pl. 26, figs. 5-10; pl. 27, figs. 1-4; Jardine and Harrington, 2008, pl. 4, fig. 11.

Tricolporopollenites sp. 4. Jardine and Harrington, 2008, p. 198-199, pl. 4, fig. 2.

Tricolporopollenites sp. 9. Jardine and Harrington, 2008, p. 199, pl. 4, fig. 5.

Dimensions. Polar diameter 27 – 38 μm , mean 32 μm (14 specimens measured); equatorial diameter 21 – 27 μm , mean 24 μm (16 specimens measured). Stover (in

Stover et al., 1966) gave a range of 36 – 41 μm for the equatorial diameter of the protologue specimens.

Remarks. The major morphological details of this species have been outlined in the genus remarks. In polar view the costae colpi appear as U-shaped bands. The ora are circular to elongate and elliptical, and are always indistinct. The exine is 1 – 2 μm thick and psilate. The equatorial diameter given by Stover (in Stover et al., 1966) is larger than for my specimens, but this may have been caused by the protologue specimens being measured in polar view (see Stover et al., 1966, p. 9). Measurements given for colpi length by Stover (in Stover et al., 1966) correspond well with my specimens, which also match well the other morphological details of this species.

Quadrupollenites vagus is similar to “*Tricolporopollenites* n. sp. A” of Tschudy 1973 in terms of grain size, shape and exine thickness, but differs from the latter species in being tetracolporate, having indistinct ora, and nexinal thickenings around the colpi. *Tetracolporopollenites* spp. have much more distinct ora.

Botanical affinity. Unknown.

Occurrence. Occurred in 58/151 samples, from the Naheola to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas. This taxon generally occurred in relative abundances of <5%, but in the lignite sample WCM/08/012 from the base of the Calvert Bluff Formation, it comprised 42% of the pollen count.

Genus *Tetracolporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Tetracolporopollenites brevis Frederiksen 1980

Plate 14, figure 1

Sapotaceoidapollenites sp. Tschudy and Van Leonen, 1970, pl. 5, figs. 4, 8a-b.

Tetracolporopollenites brevis Frederiksen, 1980a, p. 63, pl. 16, figs. 1-3; Frederiksen, 1988, p. 53, pl. 16, figs. 12-13.

Dimensions. Polar diameter 24 – 32 μm , mean 28 μm ; equatorial diameter 19 – 25 μm , mean 22 μm (four specimens measured). Frederiksen (1980a) gave a range of 24 – 42 μm for the protologue specimens.

Remarks. *Tetracolporopollenites brevis* is prolate spheroidal to prolate in shape with flattened poles and straight to slightly convex sides. The grain is tetracolporate and the colpi are 1/2 to 2/3 the length of the grain. The ora are distinct and lalongate. The exine is psilate to faintly punctate and is slightly thicker near the equator, which produces a darkened equatorial band. This species is the tetra-aperturate equivalent of the short-colpate *Tetracolporopollenites megadolium* type. For analysis *Tetracolporopollenites brevis* was counted together with *Tetracolporopollenites lesquereuxianus* and *Tetracolporopollenites megadolium*.

Botanical affinity. Sapotaceae; Frederiksen (1980a) suggested *Sideroxylon*.

Occurrence. Occurred in relative abundances of <1.3% in 5/151 samples, from the Tusahoma to the Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1988).

Tetracolporopollenites lesquereuxianus (Traverse 1955) Frederiksen 1980

Plate 14, figures 2-3

Manilkara lesquereuxiana Traverse, 1955, p. 70, figs. 12 (120-121).

Sapotaceoidapollenites cf. *S. manifestus* (Potonié 1931) Potonié et al 1950. Engelhardt, 1964, p. 76, pl. 4, fig. 49.

Sapotaceoidapollenites sp. Tschudy and Van Loenen, 1970, pl. 5, figs. 7a-b.

Tetracolporopollenites lesquereuxianus (Traverse) Frederiksen, 1980a, p. 63, pl. 16, fig. 4;

Frederiksen, 1988, p. 53-54; pl. 16, figs. 14-16.

"Sapotaceoidapollenites" lesquereuxianus (Traverse) Frederiksen, 1980b, p. 170-171, pl. 3, fig. 32.

Dimensions. Polar diameter 29 – 40 μm , mean 35 μm ; equatorial diameter 21 – 28 μm , mean 25 μm (three specimens measured). Traverse (1955) gave a range of 50 – 52 μm for the polar diameter of the protologue specimens, and a range of 37 – 49 μm for the equatorial diameter.

Remarks. This species is very similar to the specimens of *Tetracolporopollenites megadolium* that have long colpi, but differs in being tetracolporate. The colpi extend at least 3/4 the length of the grain, and as with other species in this genus the ora are lalongate and distinct. For analysis *Tetracolporopollenites lesquereuxianus* was counted together with *Tetracolporopollenites brevis* and *Tetracolporopollenites megadolium*.

Botanical affinity. Sapotaceae; Frederiksen (1980a) suggested *Manilkara*.

Occurrence. Occurred in relative abundances of <3% in 6/151 samples, in the Tallahatta and Zilpha formations on the eastern Gulf Coast. This taxon is known to range up into the Early Oligocene Vicksburg Group (Frederiksen, 1988).

TRIPROJECTATE POLLEN

Genus *Aquilapollenites* Rouse 1957 emend. Funkhouser 1961

Remarks. See Chapter 4 for genus remarks and type species.

Aquilapollenites attenuatus Funkhouser 1961

Plate 14, figure 4

Aquilapollenites attenuatus Funkhouser, 1961, p. 194, 196, pl. 2, figs. 1a-c.

Aquilapollenites spinulosus Funkhouser 1961. Jardine and Harrington, 2008

[misidentified], pl. 4, fig. 13.

Dimensions. Polar diameter 36 – 45 μm ; tips of equatorial protrusions to polar axis 28 – 34 μm (two specimens measured). Funkhouser's (1961) measured specimen had a polar axis of 43 μm , and equatorial projections 32 μm long.

Remarks. This species is isopolar and has three pairs of demicolpi. The exine is punctate, with echinae present on the polar protrusions, the tips of the equatorial protrusions, and in a band along the centre of the equatorial protrusions.

Aquilapollenites spinulosus Funkhouser 1961 has shorter equatorial protrusions, echinae covering the entire surface of the grain, and is not punctate. *Aquilapollenites polaris* is heteropolar.

Botanical affinity. Unknown.

Occurrence. Occurred in relative abundances of <1.6% in 10/151 samples, from the Porters Creek to the Hatchetigbee formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

JUGATE POLLEN

Genus *Ericipites* Wodehouse 1933

Type species. *Ericipites longisulcatus* Wodehouse 1933.

Remarks. This form genus includes pollen grains occurring as tetrahedral tetrads. The individual monads are tricolporate and have granulate to psilate exines. The colpi of neighbouring monads adjoin across the suture line. Other genera of pollen tetrads differ in the arrangement of the monads, in aperture type, in having non-adjointing apertures, or in sculpture (Nichols, 2010).

Ericipites spp.

Plate 14, figure 14

Dimensions. Tetrad diameter 23 – 30 μm ; monad diameter 11 – 20 μm (two specimens measured).

Remarks. All specimens within this taxon conform well to the diagnosis of *Ericipites*. The monads are finely scabrate to granulate, tricolporate and tightly appressed in tetrahedral tetrads. The colpi are typically unbordered and indistinct, and extend ~1/2 way to the poles. These grains were problematic to subdivide to species level, and it is not clear whether one or more individual species are present within this taxon. Given this uncertainty I have counted all *Ericipites* types together. The most similar described taxon is *Ericipites* spp. Pocknall & Nichols 1996, which may be conspecific with at least some of my specimens.

Botanical affinity. Probably Ericaceae (Pocknall and Nichols, 1996).

Occurrence. Occurred in relative abundances of <3% in 63/151 samples, from the Naheola to the Zilpha formations on the eastern Gulf Coast, and in the Calvert Bluff Formation in Texas.

ALGAL CYSTS

Genus *Pseudoschizaea* Thiergart & Frantz 1962 ex Potonié 1966 emend. Christopher
1976

Plate 14, figure 15

Remarks. According to Christopher (1976) specimens of *Pseudoschizaea* are probably the cysts of freshwater algae. This genus is distinguished by its ornamentation of circumpolar ribs that frequently spiral and/or bifurcate. The polar area is also ornamented with a series of muri, which can form a variety of patterns.

Pseudoschizaea was not included in counts or analyses, and is only illustrated here for completion and general interest. Specimens of this genus occurred in the Porters Creek, Naheola, Nanafalia and Calvert Bluff formations, and always in very low abundances.

APPENDIX 2: R CODE USED IN THE ANALYSES

##R code for Chapter 5

```
library(vegan)

##Read in data file, samples in rows, taxa in columns
rhmdata <- read.table (file = "RHM_data.txt", header=TRUE, row.
names=1)
##Read in sample info file, with formation and lithology for
each sample
rhminfo <- read.table (file = "RHM_info.txt", header=TRUE, row.
names=1)

##dataset details
dim(rhmdata)
sum(rhmdata)

##SAMPLE DATA FOR TABLE 5.1
results <- data.frame(rhminfo$Lithology, rowSums(rhmdata),
specnumber(rhmdata), t(rarefy(rhmdata, sample =
300, se = TRUE))), diversity(rhmdata, index = "invsimpson")/
specnumber(rhmdata))
colnames(results) <- c("Lithology", "N", "S", "R300", "St.
dev", "E1/D")
write.table(results, "Table5.1.txt", sep = "\t", row.names = T,
col.names = T)

##INDIVIDUAL-BASED RAREFACTION CURVES
##Compute one rarefaction curve per sample
ind.rare.AC13 <- rarefy(rhmdata[1,], sample = c(1:sum(rhmdata[1,])), se = TRUE)
ind.rare.AC12 <- rarefy(rhmdata[2,], sample = c(1:sum(rhmdata[2,])), se = TRUE)
ind.rare.AC11A <- rarefy(rhmdata[3,], sample = c(1:sum(rhmdata[3,])), se = TRUE)
ind.rare.AC009 <- rarefy(rhmdata[4,], sample = c(1:sum(rhmdata[4,])), se = TRUE)
ind.rare.AC008 <- rarefy(rhmdata[5,], sample = c(1:sum(rhmdata[5,])), se = TRUE)
ind.rare.AC006 <- rarefy(rhmdata[6,], sample = c(1:sum(rhmdata[6,])), se = TRUE)
ind.rare.AC004 <- rarefy(rhmdata[7,], sample = c(1:sum(rhmdata[7,])), se = TRUE)
ind.rare.AC002 <- rarefy(rhmdata[8,], sample = c(1:sum(rhmdata[8,])), se = TRUE)
```

##Figure 5.2

```
plot(c(1:sum(rhm.data[1,])), ind.rare.AC13[1,], xlim = c(0,
1400), ylim = c(0, 50), xlab = "Number of specimens", ylab =
"Expected richness", type = "l", las = 1)
lines(c(1:sum(rhm.data[2,])), ind.rare.AC12[1,])
lines(c(1:sum(rhm.data[3,])), ind.rare.AC11A[1,])
lines(c(1:sum(rhm.data[4,])), ind.rare.AC009[1,])
lines(c(1:sum(rhm.data[5,])), ind.rare.AC008[1,])
lines(c(1:sum(rhm.data[6,])), ind.rare.AC006[1,])
lines(c(1:sum(rhm.data[7,])), ind.rare.AC004[1,])
lines(c(1:sum(rhm.data[8,])), ind.rare.AC002[1,])
```

##RANK/ABUNDANCE PLOT

```
##Compute relative abundances for each sample, convert to
percentage, and plot as ranked abundances on a log scale
rhm.stand <- decostand(rhm.data, method = "total")
rhm.stand.percent <- rhm.stand*100
```

```
stand.AC13 <- rhm.stand.percent[1,]
stand.AC12 <- rhm.stand.percent[2,]
stand.AC11A <- rhm.stand.percent[3,]
stand.AC009 <- rhm.stand.percent[4,]
stand.AC008 <- rhm.stand.percent[5,]
stand.AC006 <- rhm.stand.percent[6,]
stand.AC004 <- rhm.stand.percent[7,]
stand.AC002 <- rhm.stand.percent[8,]
```

##Figure 5.3

```
plot(rev(sort(stand.AC009[stand.AC009>0])), type = "l", log
= "y", xlim = c(0, 50), yaxp = c(0.1, 2, 3), las = 1, xlab =
"Taxa in rank order of abundance", ylab = "Percentage of grains
counted")
lines(rev(sort(stand.AC13[stand.AC13>0])), type = "l")
lines(rev(sort(stand.AC12[stand.AC12>0])), type = "l")
lines(rev(sort(stand.AC11A[stand.AC11A>0])), type = "l")
lines(rev(sort(stand.AC008[stand.AC008>0])), type = "l")
lines(rev(sort(stand.AC006[stand.AC006>0])), type = "l")
lines(rev(sort(stand.AC004[stand.AC004>0])), type = "l")
lines(rev(sort(stand.AC002[stand.AC002>0])), type = "l")
```

##SAMPLE-BASED RAREFACTION CURVES

```
##Compute sample-based rarefaction curves for lignite and
clastic samples. Use method = "exact" to get expected richness
(y axis on graph), and method = "rarefaction" to get average
number of individuals per sample (x axis on graph) (from
$invidividuals output for "rarefaction" method - spelling is
correct!)
```

```

samp.rare.lig <- specaccum(rhm.data[rhm.info$Lithology ==
"Lignite",], method = "exact")
samp.rare.lig.ind <- specaccum(rhm.data[rhm.info$Lithology ==
"Lignite",], method = "rarefaction")

samp.rare.clast <- specaccum(rhm.data[rhm.info$Lithology ==
"Clastic",], method = "exact")
samp.rare.clast.ind <- specaccum(rhm.data[rhm.info$Lithology ==
"Clastic",], method = "rarefaction")

##Figure 5.4
plot(c(0, samp.rare.lig.ind$invididuals), c(0, samp.rare.
lig$richness), type = "l", las = 1, xlim = c(0, 3500), ylim =
c(0, 70), xlab = "Number of specimens (based on mean number of
specimens per sample)", ylab = "Expected richness")
lines(c(0, samp.rare.lig.ind$invididuals), c(0, samp.rare.
lig$richness)+1.96*c(0, samp.rare.lig$sd), lty = 2)
lines(c(0, samp.rare.lig.ind$invididuals), c(0, samp.rare.
lig$richness)-1.96*c(0, samp.rare.lig$sd), lty = 2)
lines(c(0, samp.rare.clast.ind$invididuals), c(0, samp.rare.
clast$richness))
lines(c(0, samp.rare.clast.ind$invididuals), c(0, samp.rare.
clast$richness)+1.96*c(0, samp.rare.clast$sd), lty = 2)
lines(c(0, samp.rare.clast.ind$invididuals), c(0, samp.rare.
clast$richness)-1.96*c(0, samp.rare.clast$sd), lty = 2)

##NMDS
##NMDS for non-unique taxa. Function call includes square root
transformation and Wisconsin standardisation
nm.ds.rhm <- metaMDS(rhm.data[,specnumber(rhm.data, MARGIN = 2)
> 1])

##Preliminary plots with labels
plot(nm.ds.rhm, display = "sites", type = "t", las = 1, xlab =
"NMDS axis 1", ylab = "NMDS axis 2")
plot(nm.ds.rhm, display = "species", type = "t", las = 1, xlab =
"NMDS axis 1", ylab = "NMDS axis 2")

##Figure 5.5
plot(nm.ds.rhm, display = "sites", type = "n", las = 1, xlab =
"NMDS axis 1", ylab = "NMDS axis 2", shrink = FALSE)
points(nm.ds.rhm, display = "sites", choices = c(1,2), type="p",
pch = 2, cex = 1.5, rhm.info$Lithology == "Lignite", shrink =
FALSE)
points(nm.ds.rhm, display = "sites", choices = c(1,2), type="p",
pch = 1, cex = 1.5, rhm.info$Lithology == "Clastic", shrink =
FALSE)

```

```
points(nmds.rhm, display = "species", choices = c(1,2),  
type="p", pch = 3, shrink = FALSE)
```


##R code for Chapter 6

```
library(vegan)

##Read in data file, samples in rows, taxa in columns
txal.all <- read.table (file = "TXvsAL_all.txt", header=TRUE,
row.names=1)

##Read in sample info file, with formation, lithology and sample
level for each sample
sample.info <- read.table (file = "Sample_info.txt",
header=TRUE, row.names=1)
attach(sample.info)

##RICHNESS ESTIMATION - ASSESS DEGREE OF UNDERSAMPLING
specpool(txal.all)

##SAMPLE DATA FOR TABLE 6.1
results <- dataframe(rowSums(txal.all), specnumber(txal.all),
t(rarefy(txal.all, sample = 150)))
colnames(results) <- c("N", "S", "R150")
write.table(results, "Table6.1.txt", sep = "\t", row.names = T,
col.names = T)

-----

##DATA ANALYSIS
##Remove uniques (taxa limited to one sample) - all further
analyses carried out with this dataset
txal.nosing <- txal.all[,colSums(txal.all > 0) != 1]

##ADDITIVE DIVERSITY PARTITIONING
##Read in sample level file for ADP, convert to factors, and
carry out ADP
fact.all <- read.table (file = "Sample_factors_all.txt",
header=TRUE, row.names=1)
fact.all.factors <- data.frame(
l1=as.factor(fact.all[,1]),
l2=as.factor(fact.all[,2]),
l3=as.factor(fact.all[,3]))

(txal.noSing.ADP <- adipart(txal.noSing ~ ., fact.all.factors,
index = "richness", weights = "prop", nsimul = 9999))

##Repeat for lignites only (limit dataset to lignite samples,
and remove uniques)
txal.noSing.lig <- txal.noSing[sample.info$Lithology ==
```

```

"Lignite",]
txal.noSing.lig <- txal.noSing.lig[,colSums(txal.noSing.lig >
0) > 1]

fact.lig <- read.table (file = "Sample_factors_lignite.txt",
header=TRUE, row.names=1)
fact.lig.factors <- data.frame(
l1=as.factor(fact.lig[,1]),
l2=as.factor(fact.lig[,2]),
l3=as.factor(fact.lig[,3]))

(txal.noSing.lig.ADP <- adipart(txal.noSing.lig ~ ., fact.lig.
factors, index = "richness", weights = "prop", nsimul = 9999))

##Prepare results for plotting
txal.noSing.ADP.results <- cbind(txal.noSing.ADP[[1]],
apply(txal.noSing.ADP[[2]]$simulated, 1, median))
colnames(txal.noSing.ADP.results) = c("Observed", "Expected")

txal.noSing.lig.ADP.results <- cbind(txal.noSing.lig.ADP[[1]],
apply(txal.noSing.lig.ADP[[2]]$simulated, 1, median))
colnames(txal.noSing.lig.ADP.results) = c("Observed",
"Expected")

##Figure 6.4
par(mfrow = c(1,2))
barplot(txal.noSing.ADP.results[c(1,4,5),], ylim = c(0,120),
main = "All samples", ylab = "Number of taxa")
barplot(txal.noSing.lig.ADP.results[c(1,4,5),], legend.text =
T, ylim = c(0,120), main = "Lignite samples")

##NPMANOVA
##Whole dataset
(txal.adonis.form <- adonis(txal.noSing.dist ~ Formation, data
= sample.info, permutations = 9999))
(txal.adonis.form.lith <- adonis(txal.noSing.dist ~
Formation*Lithology, data = sample.info, permutations = 9999))

##Lignites only
sample.info.lig <- sample.info[sample.info$Lithology ==
"Lignite",]
txal.noSing.lig.dist <- vegdist(txal.noSing.lig, method =
"jaccard", binary = T)
(txal.lig.adonis <- adonis(txal.noSing.lig.dist ~ Formation,
data = sample.info.lig, permutations = 9999))

```

```

##NMDS ANALYSIS
##Whole dataset
meta.txal <- metaMDS(txal.nosing, distance = "jaccard", binary
= TRUE)

##Figure 6.5
plot(meta.txal, display = c("sites"), choices = c(1,2),
type="n", shrink=FALSE, xlab = "NMDS Axis 1", ylab = "NMDS Axis
2")
points(meta.txal, display = "sites", choices = c(1,2),
shrink=FALSE, pch = 1, Formation == "Tuscahoma" & Lithology ==
"Lignite")
points(meta.txal, display = "sites", choices = c(1,2),
shrink=FALSE, pch = 21, bg = "black", Formation == "Calvert.
Bluff" & Lithology == "Lignite")
points(meta.txal, display = "sites", choices = c(1,2),
shrink=FALSE, pch = 24, bg = "black", Formation == "Calvert.
Bluff" & Lithology == "Clastic")
points(meta.txal, display = "sites", choices = c(1,2),
shrink=FALSE, pch = 2, Formation == "Tuscahoma" & Lithology ==
"Clastic")

##NMDS for Calvert Bluff Formation
calvert <- txal.noSing[Formation == "Calvert.Bluff",]
calvert <- calvert[,colSums(calvert > 0) > 1]
calvert.info <- sample.info[Formation == "Calvert.Bluff",]
meta.calvert <- metaMDS(calvert, distance = "jaccard", binary =
T)

##Figure 6.6A
plot(meta.calvert, display = "sites", choices = c(1,2),
type="n", shrink=FALSE, xlab = "NMDS Axis 1", ylab = "NMDS Axis
2")
points(meta.calvert, display = "sites", choices = c(1,2),
type="p", shrink=FALSE, pch = 24, bg = "black", (calvert.
info$Locality == "NAC" | calvert.info$Locality == "UCB" |
calvert.info$Locality == "BGC") & calvert.info$Lithology ==
"Clastic")
points(meta.calvert, display = "sites", choices = c(1,2),
type="p", shrink=FALSE, pch = 21, bg = "black", (calvert.
info$Locality == "NAC" | calvert.info$Locality == "UCB" |
calvert.info$Locality == "BGC") & calvert.info$Lithology ==
"Lignite")
points(meta.calvert, display = "sites", choices = c(1,2),
type="p", shrink=FALSE, pch = 2, bg = "black", (calvert.
info$Locality == "WCM" | calvert.info$Locality == "SM") &
calvert.info$Lithology == "Clastic")

```

```

points(meta.calvert, display = "sites", choices = c(1,2),
type="p", shrink=FALSE, pch = 1, bg = "black", (calvert.
info$Locality == "WCM" | calvert.info$Locality == "SM") &
calvert.info$Lithology == "Lignite")

##NMDS for Tuscahoma Formation
tuscahoma <- txal.noSing[Formation == "Tuscahoma",]
tuscahoma <- tuscahoma[,colSums(tuscahoma > 0) > 1]
tusc.info <- sample.info[Formation == "Tuscahoma",]
meta.tusc <- metaMDS(tuscahoma, distance = "jaccard", binary =
T)

##Figure 6.6B
plot(meta.tusc, display = "sites", choices = c(1,2), type="n",
shrink=FALSE, main = "NMDS plot showing Tuscahoma samples",
xlab = "NMDS Axis 1", ylab = "NMDS Axis 2")
text(meta.tusc, display = "sites", choices = c(1,2), labels =
c(26:1, "GH00/AC/012", "GH00/AC/009"), shrink=FALSE)
points(meta.tusc, display = "sites", choices = c(1,2), pch=21,
cex = 4, tusc.info$Lithology == "Lignite", shrink=FALSE)

##CLUSTER ANALYSIS
##Distance matrix and cluster analysis for samples
txal.sites.dist <- vegdist(txal.noSing, method = "jaccard",
binary = TRUE)
txal.sites.clust <- hclust(txal.sites.dist, method = "average")

##Distance matrix and cluster analysis for taxa
txal.species.dist <- vegdist(t(txal.noSing), method =
"jaccard", binary = TRUE)
txal.species.clust <- hclust(txal.species.dist, method =
"average")

##Figure 6.7 - dendrograms exported to Illustrator for figure
preparation
plot(txal.sites.clust)
plot(txal.sites.clust, labels = Formation)
plot(txal.sites.clust, labels = Lithology)

plot(txal.species.clust)

##COMPARISON OF COMMON TAXA
calvert <- txal.noSing[Formation == "Calvert.Bluff",]
calv.inc <- colSums(calvert > 0)
calv.inc <- sort(calv.inc, decreasing = T)

```

```

tuscahoma <- txal.noSing[Formation == "Tuscahoma",]
tusc.inc <- colSums(tuscahoma > 0)
tusc.inc <- sort(tusc.inc, decreasing = T)

##Figure 6.8
par(mfrow = c(2,1))
barplot(calv.inc[1:15], las = 2, cex.names = 0.7, font.axis =
3, ylim = c(0,30), ylab = "Number of samples", main = "Calvert
Bluff Fm., TX")
barplot(tusc.inc[1:15], las = 2, cex.names = 0.7, font.axis =
3, ylim = c(0,30), ylab = "Number of samples", xlab = "Taxa",
main = "Tuscahoma Fm., MS/AL")

-----

##COMPARISON WITH HOLOCENE DATA
##Construct geographical inter-sample distance matrices
library(spdep)

##Temperate data, coordinates for each lake core in rows
temp <- read.table (file = "Temperate_coords.txt", header=TRUE,
row.names=1)
temp <- as.matrix(temp)
temp.knn <- knearneigh(temp, k=10, longlat=TRUE)
temp.nb <- knn2nb(temp.knn)
temp.dist <- nbdists(temp.nb, temp, longlat = TRUE)
temp.dist.matrix <- matrix(unlist(temp.dist), byrow = T, nrow =
11)

##Save matrix for formatting in Excel (e.g. adding in zero
distances on the diagonal)
write.table(temp.dist.matrix, "Temp_dist.txt", sep = "\t", row.
names = T, col.names = T)

##Repeat for each of other datasets - warm mixed, tropical,
temperate with combined sites, warm mixed with combined sites

##Regression of inter-sample compositional similarity onto
inter-sample geographic distance
##Temperate compositional data matrix
temperate.comm <- read.table (file = "Temperate.txt",
header=TRUE, row.names=1)
temperate.comm <- temperate.comm[,colSums(temperate.comm > 0)
!= 1]
temperate.comm.dist <- vegdist(temperate.comm, method =
"jaccard", binary = TRUE)
##Take natural log and convert from distance to similarity

```

```

temperate.comm.dist <- log(1-temperate.comm.dist)
temperate.comm.dist.vec <- as.vector(temperate.comm.dist)

##Temperate geographic distance matrix (now correctly
formatted)
temperate.geog <- read.table (file = "Temperate_dist.txt",
header=TRUE, row.names=1)
temperate.geog.dist <- as.dist(temperate.geog)
temperate.geog.dist.vec <- as.vector(temperate.geog.dist)

##Regression
temperate.obs.ind <- lm(temperate.comm.dist.vec ~ temperate.
geog.dist.vec)
summary(temperate.obs.ind)

##Randomization test of significance
temperate.r.squared <- numeric(9999)
temperate.F <- numeric(9999)
for(i in 1:9999) {
  model <- lm(sample(temperate.comm.dist.vec,
length(temperate.comm.dist.vec)) ~ temperate.geog.dist.vec)
  temperate.r.squared[i] <- summary(model)[[8]]
  temperate.F[i] <- summary(model)[[10]][1]
}

##Significance of R^2 value
temperate.r.squared <- c(temperate.r.squared,
summary(temperate.obs.ind)[[8]])
1-sum(temperate.r.squared<summary(temperate.obs.ind)[[8]])/
length(temperate.r.squared)

##Significance of F value
temperate.F <- c(temperate.F, summary(temperate.obs.ind)[[10]]
[1])
1-(sum(temperate.F<summary(temperate.obs.ind)[[10]][1])/
length(temperate.F))

##Should be the same!
##Again, repeated for each of the other Holocene datasets, so
that each one has a regression model with significance

##Calculate GCP Paleocene inter-formation, inter-sample
compositional similarity
##Limit to clastic samples, and remove unique taxa (i.e. now
limited to one sample)
txal.nosing.clast <- txal.nosing[Lithology == "Clastic",]
txal.nosing.clast <- txal.nosing.clast[,colSums(txal.nosing.

```

```

clast > 0) > 1]
txal.nosing.clast.dist <- vegdist(txal.nosing.clast, method =
"jaccard", binary = TRUE)
txal.nosing.clast.dist.matrix <- as.matrix(txal.nosing.clast.
dist)
##Only inter-formation distances wanted:
txal.nosing.clast.dist.vec <- as.vector(txal.nosing.clast.dist.
matrix[23:45,1:22])
txal.nosing.clast.dist.vec <- log(1-txal.nosing.clast.dist.vec)

##Mean similarity
mean(txal.nosing.clast.dist.vec)

##Test for normality
shapiro.test(txal.nosing.clast.dist.vec)

##Non-parametric (bootstrapped) 95% CIs
boot.mean.clast <- numeric(10000)
for(i in 1:10000) boot.mean.clast[i] <- mean(sample(txal.
nosing.clast.dist.vec, length(txal.nosing.clast.dist.vec),
replace = T))
quantile(boot.mean.clast, c(.025, .975))

##Also repeated with whole dataset (e.g. with clastics and
lignites, using txal.nosing rather than txal.nosing.clast)

##Figure 6.10A
plot(tropics.geog.dist.vec, tropics.comm.dist.vec, col =
"grey40", ylim = c(-1.4, 0), xlim = c(0, 1300), xlab =
"Distance (km)", ylab = "ln Jaccard similarity")
points(warm.mixed.geog.dist.vec, warm.mixed.comm.dist.vec,
pch=0, col = "grey40")
points(temperate.geog.dist.vec, temperate.comm.dist.vec, pch=2,
col = "grey40")
abline(tropics.obs.ind)
abline(warm.mixed.obs.ind, lty = 2)
abline(temperate.obs.ind, lty = 3)
points(819, -0.8317677, pch = 4)
lines(c(819, 819), c(-0.8442460, -0.8194573))

##Figure 6.10B
plot(temperate.comb.geog.dist.vec, temperate.comb.comm.dist.
vec, pch=2, col = "grey40", ylim= c(-1, 0), xlab = "Distance
(km)", ylab = "ln Jaccard similarity")
points(warm.mixed.comb.geog.dist.vec, warm.mixed.comb.comm.
dist.vec, pch=0, col = "grey40")
abline(temperate.comb.obs.ind, lty = 3)

```

```
abline(warm.mixed.comb.obs.ind, lty = 2)
points(819, -0.8317677, pch = 4)
lines(c(819, 819), c(-0.8442460, -0.8194573))
```


##R code for Chapter 7

```
library(vegan)

##Read in data files and sample info files for GCP and Colombia
(samples in rows)
gcp <- read.table (file = "GCP_data.txt", header=TRUE, row.
names=1)
gcp.info <- read.table (file = "GCP_sample_info.txt",
header=TRUE, row.names=1)

col <- read.table (file = "Colombian_data.txt", header=TRUE,
row.names=1)
col.info <- read.table (file = "Colombian_sample_info.txt",
header=TRUE, row.names=1)

##Dataset summaries - number of specimens, samples and taxa
sum(gcp)
dim(gcp)
sum(col)
dim(col)

##SAMPLE DATA FOR TABLE 7.1
results <- data.frame(rowSums(gcp), specnumber(gcp),
t(rarefy(gcp, sample = 50, se = TRUE)), t(rarefy(gcp, sample =
300, se = TRUE)), t(estimateR(gcp)[,2:3]), diversity(gcp, index
= "invsimpson")/specnumber(gcp))
colnames(results) <- c("N", "S", "R50", "R50 s.e.", "R300",
"R300 s.e.", "Chao1", "Chao1 s.e.", "E1/D")
write.table(results, "Table7.1.txt", sep = "\t", row.names = T,
col.names = T)

##INDIVIDUAL-BASED ANALYSES (RAREFACTION, ESTIMATION AND
EVENNESS)
##GCP
gcp.rare.ind.50 <- rarefy(gcp, 50, se = TRUE)
gcp.rare.ind.300 <- rarefy(gcp, 300, se = TRUE)
gcp.spec.num <- specnumber(gcp)
gcp.ind.num <- rowSums(gcp)
gcp.sim <- diversity(gcp, "simpson")
gcp.invsim <- diversity(gcp, "invsimpson")
gcp.est.ind <- estimateR(gcp)
gcp.results.ind <- rbind(gcp.ind.num, gcp.spec.num, gcp.rare.
ind.50, gcp.rare.ind.300, gcp.est.ind, gcp.sim, gcp.invsim)
gcp.results.ind <- t(gcp.results.ind)
colnames(gcp.results.ind) <- c("N", "S", "R^50", "R^50.se",
"R^300", "R^300.se", "S", "Chao1", "Chao1.se", "ACE", "ACE.se",
```

```

"1-D", "1/D")

##Colombia
col.rare.ind.50 <- rarefy(col, 50, se = TRUE)
col.rare.ind.300 <- rarefy(col, 300, se = TRUE)
col.spec.num <- specnumber(col)
col.ind.num <- rowSums(col)
col.sim <- diversity(col, "simpson")
col.invsim <- diversity(col, "invsimpson")
col.est.ind <- estimateR(col)
col.results.ind <- rbind(col.ind.num, col.spec.num, col.rare.
ind.50, col.rare.ind.300, col.est.ind, col.sim, col.invsim)
col.results.ind <- t(col.results.ind)
colnames(col.results.ind) <- c("N", "S", "R^50", "R^50.se",
"R^300", "R^300.se", "S", "Chao1", "Chao1.se", "ACE", "ACE.se",
"1-D", "1/D")

##Plotting of results (in composite figures)
results.total <- rbind(col.results, gcp.results)
info.total <- rbind(col.info, gcp.info)
sampling.bins <- c("GCP.MP", "COL.MP", "GCP.LP", "COL.LP",
"GCP.EE", "COL.EE", "GCP.ME", "COL.ME")

##Three boxplots stacked one on top of the other - rare50,
chao1, sim.even.

##Figure 7.1
##Upper plot
par(fig = c(0, 1, 11.1/16.8, 1))
par(mar = c(0, 5, 2, 2))
boxplot(results.total[results.total[,4] != 0,3] ~ info.
total[results.total[,4] != 0,4], ylab = "R^50 richness", boxwex
= 0.6, xaxt = "n", las = 1, names = NULL, notch = T)

##Middle plot
par(fig = c(0, 1, 6.4/16.8, 11.1/16.8), new = T)
par(mar = c(0, 5, 0, 2))
boxplot(results.total[,8] ~ info.total[,4], ylab = "Chao1
richness", boxwex = 0.6, xaxt = "n", las = 1, names = NULL,
notch = T)

##Lower plot
par(fig = c(0, 1, 0, 6.4/16.8), new = T)
par(mar = c(3.3, 5, 0, 2))
boxplot(results.total[,13]/results.total[,2] ~ info.total[,4],
ylim = c(0,0.9), ylab = "Evenness: (1/D)/S", boxwex = 0.6, las
= 1, names = sampling.bins, notch = T)

```

```

##SAMPLE-BASED RAREFACTION
##For GCP and Colombia within each time bin
gcp.MP.specaccum <- specaccum(gcp[gcp.info$Time.bin == "GCP.
MP",])
gcp.LP.specaccum <- specaccum(gcp[gcp.info$Time.bin == "GCP.
LP",])
gcp.EE.specaccum <- specaccum(gcp[gcp.info$Time.bin == "GCP.
EE",])
gcp.ME.specaccum <- specaccum(gcp[gcp.info$Time.bin == "GCP.
ME",])

gcp.MP.rare <- specaccum(gcp[gcp.info$Time.bin == "GCP.MP",],
method = "rarefaction")
gcp.LP.rare <- specaccum(gcp[gcp.info$Time.bin == "GCP.LP",],
method = "rarefaction")
gcp.EE.rare <- specaccum(gcp[gcp.info$Time.bin == "GCP.EE",],
method = "rarefaction")
gcp.ME.rare <- specaccum(gcp[gcp.info$Time.bin == "GCP.ME",],
method = "rarefaction")

col.MP.specaccum <- specaccum(col[col.info$Time.bin == "Col.
MP",])
col.LP.specaccum <- specaccum(col[col.info$Time.bin == "Col.
LP",])
col.EE.specaccum <- specaccum(col[col.info$Time.bin == "Col.
EE",])
col.ME.specaccum <- specaccum(col[col.info$Time.bin == "Col.
ME",])

col.MP.rare <- specaccum(col[col.info$Time.bin == "Col.MP",],
method = "rarefaction")
col.LP.rare <- specaccum(col[col.info$Time.bin == "Col.LP",],
method = "rarefaction")
col.EE.rare <- specaccum(col[col.info$Time.bin == "Col.EE",],
method = "rarefaction")
col.ME.rare <- specaccum(col[col.info$Time.bin == "Col.ME",],
method = "rarefaction")

##Figure 7.2A
plot(gcp.MP.rare$invididuals, gcp.MP.specaccum$richness, type
= "l", xlim = c(0, 20000), ylim = c(0, 150), xlab = "", ylab =
"Within-Age richness", col = "plum")

lines(gcp.LP.rare$invididuals, gcp.LP.specaccum$richness, col
= "green")
lines(gcp.LP.rare$invididuals, gcp.
LP.specaccum$richness+1.96*gcp.LP.specaccum$sd, lty = 2, col =

```

```

"green")
lines(gcp.LP.rare$invidivuduals, gcp.LP.specaccum$richness-
1.96*gcp.LP.specaccum$sd, lty = 2, col = "green")

lines(gcp.EE.rare$invidivuduals, gcp.EE.specaccum$richness, col
= "blue")
lines(gcp.EE.rare$invidivuduals, gcp.
EE.specaccum$richness+1.96*gcp.EE.specaccum$sd, lty = 2, col =
"blue")
lines(gcp.EE.rare$invidivuduals, gcp.EE.specaccum$richness-
1.96*gcp.EE.specaccum$sd, lty = 2, col = "blue")

lines(gcp.ME.rare$invidivuduals, gcp.ME.specaccum$richness, col
= "red")

##Figure 7.2B
plot(col.MP.rare$invidivuduals, col.MP.specaccum$richness, type
= "l", xlim = c(0, 20000), ylim = c(0, 500), xlab = "Number of
specimens (based on mean number of specimens per sample)", ylab
= "Within-Age richness", col = "plum")
lines(col.MP.rare$invidivuduals, col.
MP.specaccum$richness+1.96*col.MP.specaccum$sd, lty = 2, col =
"plum")
lines(col.MP.rare$invidivuduals, col.MP.specaccum$richness-
1.96*col.MP.specaccum$sd, lty = 2, col = "plum")

lines(col.LP.rare$invidivuduals, col.LP.specaccum$richness, col
= "green")

lines(col.EE.rare$invidivuduals, col.EE.specaccum$richness, col
= "blue")

lines(col.ME.rare$invidivuduals, col.ME.specaccum$richness, col
= "red")
lines(col.MEE.rare$invidivuduals, col.
ME.specaccum$richness+1.96*col.ME.specaccum$sd, lty = 2, col =
"red")
lines(col.ME.rare$invidivuduals, col.ME.specaccum$richness-
1.96*col.ME.specaccum$sd, lty = 2, col = "red")

##For GCP and Colombia, by locality within each time bin
gcp.MP <- gcp[gcp.info$Time.bin == "GCP.MP",]
gcp.LP <- gcp[gcp.info$Time.bin == "GCP.LP",]
gcp.EE <- gcp[gcp.info$Time.bin == "GCP.EE",]
gcp.ME <- gcp[gcp.info$Time.bin == "GCP.ME",]

gcp.info.MP <- gcp.info[gcp.info$Time.bin == "GCP.MP",]

```

```

gcp.info.LP <- gcp.info[gcp.info$Time.bin == "GCP.LP",]
gcp.info.EE <- gcp.info[gcp.info$Time.bin == "GCP.EE",]
gcp.info.ME <- gcp.info[gcp.info$Time.bin == "GCP.ME",]

col.MP <- col[col.info$Time.bin == "Col.MP",]
col.LP <- col[col.info$Time.bin == "Col.LP",]
col.EE <- col[col.info$Time.bin == "Col.EE",]
col.ME <- col[col.info$Time.bin == "Col.ME",]

col.info.MP <- col.info[col.info$Time.bin == "Col.MP",]
col.info.LP <- col.info[col.info$Time.bin == "Col.LP",]
col.info.EE <- col.info[col.info$Time.bin == "Col.EE",]
col.info.ME <- col.info[col.info$Time.bin == "Col.ME",]

##Middle Paleocene
gcp.cores.MP <- unique(gcp.info.MP$Core)
gcp.rare.MP.exact <- vector("list", length = length(gcp.cores.
MP))
gcp.rare.MP.ind <- vector("list", length = length(gcp.cores.
MP))
for (i in 1:length(gcp.cores.MP)) gcp.rare.MP.exact[[i]] <-
specaccum(gcp.MP[gcp.info.MP$Core == gcp.cores.MP[i],])
for (i in 1:length(gcp.cores.MP)) gcp.rare.MP.ind[[i]] <-
specaccum(gcp.MP[gcp.info.MP$Core == gcp.cores.MP[i],], method
= "rarefaction")

col.cores.MP <- unique(col.info.MP$Core)
col.rare.MP.exact <- vector("list", length = length(col.cores.
MP))
col.rare.MP.ind <- vector("list", length = length(col.cores.
MP))
for (i in 1:length(col.cores.MP)) col.rare.MP.exact[[i]] <-
specaccum(col.MP[col.info.MP$Core == col.cores.MP[i],])
for (i in 1:length(col.cores.MP)) col.rare.MP.ind[[i]] <-
specaccum(col.MP[col.info.MP$Core == col.cores.MP[i],], method
= "rarefaction")

##Late Paleocene
gcp.cores.LP <- unique(gcp.info.LP$Core)
gcp.rare.LP.exact <- vector("list", length = length(gcp.cores.
LP))
gcp.rare.LP.ind <- vector("list", length = length(gcp.cores.
LP))
for (i in 1:length(gcp.cores.LP)) gcp.rare.LP.exact[[i]] <-
specaccum(gcp.LP[gcp.info.LP$Core == gcp.cores.LP[i],])
for (i in 1:length(gcp.cores.LP)) gcp.rare.LP.ind[[i]] <-
specaccum(gcp.LP[gcp.info.LP$Core == gcp.cores.LP[i],], method

```

```

= "rarefaction")

col.cores.LP <- unique(col.info.LP$Core)
col.rare.LP.exact <- vector("list", length = length(col.cores.
LP))
col.rare.LP.ind <- vector("list", length = length(col.cores.
LP))
for (i in 1:length(col.cores.LP)) col.rare.LP.exact[[i]] <-
specaccum(col.LP[col.info.LP$Core == col.cores.LP[i],])
for (i in 1:length(col.cores.LP)) col.rare.LP.ind[[i]] <-
specaccum(col.LP[col.info.LP$Core == col.cores.LP[i],], method
= "rarefaction")

##Early Eocene
gcp.cores.EE <- unique(gcp.info.EE$Core)
gcp.rare.EE.exact <- vector("list", length = length(gcp.cores.
EE))
gcp.rare.EE.ind <- vector("list", length = length(gcp.cores.
EE))
for (i in 1:length(gcp.cores.EE)) gcp.rare.EE.exact[[i]] <-
specaccum(gcp.EE[gcp.info.EE$Core == gcp.cores.EE[i],])
for (i in 1:length(gcp.cores.EE)) gcp.rare.EE.ind[[i]] <-
specaccum(gcp.EE[gcp.info.EE$Core == gcp.cores.EE[i],], method
= "rarefaction")

col.cores.EE <- unique(col.info.EE$Core)
col.rare.EE.exact <- vector("list", length = length(col.cores.
EE))
col.rare.EE.ind <- vector("list", length = length(col.cores.
EE))
for (i in 1:length(col.cores.EE)) col.rare.EE.exact[[i]] <-
specaccum(col.EE[col.info.EE$Core == col.cores.EE[i],])
for (i in 1:length(col.cores.EE)) col.rare.EE.ind[[i]] <-
specaccum(col.EE[col.info.EE$Core == col.cores.EE[i],], method
= "rarefaction")

##Middle Eocene
gcp.cores.ME <- unique(gcp.info.ME$Core)
gcp.rare.ME.exact <- vector("list", length = length(gcp.cores.
ME))
gcp.rare.ME.ind <- vector("list", length = length(gcp.cores.
ME))
for (i in 1:length(gcp.cores.ME)) gcp.rare.ME.exact[[i]] <-
specaccum(gcp.ME[gcp.info.ME$Core == gcp.cores.ME[i],])
for (i in 1:length(gcp.cores.ME)) gcp.rare.ME.ind[[i]] <-
specaccum(gcp.ME[gcp.info.ME$Core == gcp.cores.ME[i],], method
= "rarefaction")

```

```

col.cores.ME <- unique(col.info.ME$Core)
col.rare.ME.exact <- vector("list", length = length(col.cores.
ME))
col.rare.ME.ind <- vector("list", length = length(col.cores.
ME))
for (i in 1:length(col.cores.ME)) col.rare.ME.exact[[i]] <-
specaccum(col.ME[col.info.ME$Core == col.cores.ME[i],])
for (i in 1:length(col.cores.ME)) col.rare.ME.ind[[i]] <-
specaccum(col.ME[col.info.ME$Core == col.cores.ME[i],], method
= "rarefaction")

##Figure 7.3
par(mfrow = c(2,2))
par(oma = c(3,2,0,0))
par(mar = c(2, 3, 2, 1))
plot(seq(0, 5000, 500), seq(0, 250, 25), type = "n", xlab = "",
ylab = "", main = "Middle Paleocene sites")
for (i in 1:length(col.cores.MP)) lines(col.rare.
MP.ind[[i]]$invididuals, col.rare.MP.exact[[i]]$richness, col
= "grey40", lty = 2)
for (i in 1:length(gcp.cores.MP)) lines(gcp.rare.
MP.ind[[i]]$invididuals, gcp.rare.MP.exact[[i]]$richness)

par(mar = c(2, 3, 2, 1))
plot(seq(0, 12000, 1200), seq(0, 250, 25), type = "n", xlab =
"", ylab = "", main = "Late Paleocene sites")
for (i in 1:length(col.cores.LP)) lines(col.rare.
LP.ind[[i]]$invididuals, col.rare.LP.exact[[i]]$richness, col
= "grey40", lty = 2)
for (i in 1:length(gcp.cores.LP)) lines(gcp.rare.
LP.ind[[i]]$invididuals, gcp.rare.LP.exact[[i]]$richness)

par(mar = c(2, 3, 2, 1))
plot(seq(0, 5000, 500), seq(0, 250, 25), type = "n", xlab = "",
ylab = "", main = "Early Eocene sites")
for (i in 1:length(col.cores.EE)) lines(col.rare.
EE.ind[[i]]$invididuals, col.rare.EE.exact[[i]]$richness, col
= "grey40", lty = 2)
for (i in 1:length(gcp.cores.EE)) lines(gcp.rare.
EE.ind[[i]]$invididuals, gcp.rare.EE.exact[[i]]$richness)

par(mar = c(2, 3, 2, 1))
plot(seq(0, 5000, 500), seq(0, 250, 25), type = "n", xlab = "",
ylab = "", main = "Middle Eocene sites")
for (i in 1:length(col.cores.ME)) lines(col.rare.
ME.ind[[i]]$invididuals, col.rare.ME.exact[[i]]$richness, col
= "grey40", lty = 2)

```

```

for (i in 1:length(gcp.cores.ME)) lines(gcp.rare.
ME.ind[[i]]$invidividuals, gcp.rare.ME.exact[[i]]$richness)

title(xlab = "Number of individuals (based on mean number of
individuals per sample)", ylab = "Species richness", outer =
T, line = 1)

##INCIDENCE-BASED RICHNESS ESTIMATION - CHAO2
##For GCP and Colombia within each time bin
gcp.est.MP <- poolaccum(gcp.MP)
gcp.est.LP <- poolaccum(gcp.LP)
gcp.est.EE <- poolaccum(gcp.EE)
gcp.est.ME <- poolaccum(gcp.ME)

gcp.chao.MP <- summary(gcp.est.MP, display = "chao")
gcp.chao.LP <- summary(gcp.est.LP, display = "chao")
gcp.chao.EE <- summary(gcp.est.EE, display = "chao")
gcp.chao.ME <- summary(gcp.est.ME, display = "chao")

col.est.MP <- poolaccum(col.MP)
col.est.LP <- poolaccum(col.LP)
col.est.EE <- poolaccum(col.EE)
col.est.ME <- poolaccum(col.ME)

col.chao.MP <- summary(col.est.MP, display = "chao")
col.chao.LP <- summary(col.est.LP, display = "chao")
col.chao.EE <- summary(col.est.EE, display = "chao")
col.chao.ME <- summary(col.est.ME, display = "chao")

##Figure 7.4A
plot(gcp.chao.MP[[1]][,1], gcp.chao.MP[[1]][,2], type = "l",
xlim = c(0, 60), ylim = c(0, 220), xlab = "", ylab = "Chao2
estimated species richness", col = "plum")
lines(gcp.chao.MP[[1]][,1], gcp.chao.MP[[1]][,3], lty = 2, col
= "plum")
lines(gcp.chao.MP[[1]][,1], gcp.chao.MP[[1]][,4], lty = 2, col
= "plum")

lines(gcp.chao.LP[[1]][,1], gcp.chao.LP[[1]][,2], col =
"green")
lines(gcp.chao.LP[[1]][,1], gcp.chao.LP[[1]][,3], lty = 2, col
= "green")
lines(gcp.chao.LP[[1]][,1], gcp.chao.LP[[1]][,4], lty = 2, col
= "green")

lines(gcp.chao.EE[[1]][,1], gcp.chao.EE[[1]][,2], col = "blue")
lines(gcp.chao.EE[[1]][,1], gcp.chao.EE[[1]][,3], lty = 2, col

```



```

= "blue")
lines(gcp.chao.EE[[1]][,1], gcp.chao.EE[[1]][,4], lty = 2, col
= "blue")

lines(gcp.chao.ME[[1]][,1], gcp.chao.ME[[1]][,2], col = "red")
lines(gcp.chao.ME[[1]][,1], gcp.chao.ME[[1]][,3], lty = 2, col
= "red")
lines(gcp.chao.ME[[1]][,1], gcp.chao.ME[[1]][,4], lty = 2, col
= "red")

##Figure 7.4B
plot(col.chao.MP[[1]][,1], col.chao.MP[[1]][,2], type = "l",
xlim = c(0, 120), ylim = c(0, 900), xlab = "Number of samples",
ylab = "Chao2 estimated species richness", col = "plum")
lines(col.chao.MP[[1]][,1], col.chao.MP[[1]][,3], lty = 2, col
= "plum")
lines(col.chao.MP[[1]][,1], col.chao.MP[[1]][,4], lty = 2, col
= "plum")

lines(col.chao.LP[[1]][,1], col.chao.LP[[1]][,2], col =
"green")
lines(col.chao.LP[[1]][,1], col.chao.LP[[1]][,3], lty = 2, col
= "green")
lines(col.chao.LP[[1]][,1], col.chao.LP[[1]][,4], lty = 2, col
= "green")

lines(col.chao.EE[[1]][,1], col.chao.EE[[1]][,2], col = "blue")
lines(col.chao.EE[[1]][,1], col.chao.EE[[1]][,3], lty = 2, col
= "blue")
lines(col.chao.EE[[1]][,1], col.chao.EE[[1]][,4], lty = 2, col
= "blue")

lines(col.chao.ME[[1]][,1], col.chao.ME[[1]][,2], col = "red")
lines(col.chao.ME[[1]][,1], col.chao.ME[[1]][,3], lty = 2, col
= "red")
lines(col.chao.ME[[1]][,1], col.chao.ME[[1]][,4], lty = 2, col
= "red")

##For GCP and Colombia, by locality within each time bin
##Middle Paleocene
gcp.est.MP.core <- vector("list", length = length(gcp.cores.
MP))
for (i in 1:length(gcp.cores.MP)) gcp.est.MP.core[[i]] <-
poolaccum(gcp.MP[gcp.info.MP$Core == gcp.cores.MP[i],], minsize
= 1)
col.est.MP.core <- vector("list", length = length(col.cores.
MP))

```

```

for (i in 1:length(col.cores.MP)) col.est.MP.core[[i]] <-
poolaccum(col.MP[col.info.MP$Core == col.cores.MP[i],], minsize
= 1)

##Late Paleocene
gcp.est.LP.core <- vector("list", length = length(gcp.cores.
LP))
for (i in 1:length(gcp.cores.LP)) gcp.est.LP.core[[i]] <-
poolaccum(gcp.LP[gcp.info.LP$Core == gcp.cores.LP[i],], minsize
= 1)
col.est.LP.core <- vector("list", length = length(col.cores.
LP))
for (i in 1:length(col.cores.LP)) col.est.LP.core[[i]] <-
poolaccum(col.LP[col.info.LP$Core == col.cores.LP[i],], minsize
= 1)

##Early Eocene - NB have to remove Colombian cores with only
one sample
gcp.est.EE.core <- vector("list", length = length(gcp.cores.
EE))
for (i in 1:length(gcp.cores.EE)) gcp.est.EE.core[[i]] <-
poolaccum(gcp.EE[gcp.info.EE$Core == gcp.cores.EE[i],], minsize
= 1)

col.cores.EE <- col.cores.EE[-c(3, 4, 7)]
col.est.EE.core <- vector("list", length = length(col.cores.
EE))
for (i in 1:length(col.cores.EE)) col.est.EE.core[[i]] <-
poolaccum(col.EE[col.info.EE$Core == col.cores.EE[i],], minsize
= 1)

##Middle Eocene - NB have to remove Colombian cores with only
one sample
gcp.est.ME.core <- vector("list", length = length(gcp.cores.
ME))
for (i in 1:length(gcp.cores.ME)) gcp.est.ME.core[[i]] <-
poolaccum(gcp.ME[gcp.info.ME$Core == gcp.cores.ME[i],], minsize
= 1)

col.cores.ME <- col.cores.ME[-2]
col.est.ME.core <- vector("list", length = length(col.cores.
ME))
for (i in 1:length(col.cores.ME)) col.est.ME.core[[i]] <-
poolaccum(col.ME[col.info.ME$Core == col.cores.ME[i],], minsize
= 1)

```

##Figure 7.5

```

par(mfrow = c(2,2))
par(oma = c(3,2,3,0))
par(mar = c(2, 3, 2, 1))

plot(seq(0, 40, 4), seq(0, 500, 50), type = "n", xlab = "",
ylab = "", main = "Middle Paleocene sites")
for (i in 1:length(col.cores.MP)) lines(summary(col.est.
MP.core[[i]], display = "chao")[[1]][,1], summary(col.est.
MP.core[[i]], display = "chao")[[1]][,2], col = "grey40", lty =
2)
for (i in 1:length(gcp.cores.MP)) lines(summary(gcp.est.
MP.core[[i]], display = "chao")[[1]][,1], summary(gcp.est.
MP.core[[i]], display = "chao")[[1]][,2])

plot(seq(0, 40, 4), seq(0, 500, 50), type = "n", xlab = "",
ylab = "", main = "Late Paleocene sites")
for (i in 1:length(col.cores.LP)) lines(summary(col.est.
LP.core[[i]], display = "chao")[[1]][,1], summary(col.est.
LP.core[[i]], display = "chao")[[1]][,2], col = "grey40", lty =
2)
for (i in 1:length(gcp.cores.LP)) lines(summary(gcp.est.
LP.core[[i]], display = "chao")[[1]][,1], summary(gcp.est.
LP.core[[i]], display = "chao")[[1]][,2])

plot(seq(0, 40, 4), seq(0, 500, 50), type = "n", xlab = "",
ylab = "", main = "Early Eocene sites")
for (i in 1:length(col.cores.EE)) lines(summary(col.est.
EE.core[[i]], display = "chao")[[1]][,1], summary(col.est.
EE.core[[i]], display = "chao")[[1]][,2], col = "grey40", lty =
2)
for (i in 1:length(gcp.cores.EE)) lines(summary(gcp.est.
EE.core[[i]], display = "chao")[[1]][,1], summary(gcp.est.
EE.core[[i]], display = "chao")[[1]][,2])

plot(seq(0, 40, 4), seq(0, 500, 50), type = "n", xlab = "",
ylab = "", main = "Middle Eocene sites")
for (i in 1:length(col.cores.ME)) lines(summary(col.est.
ME.core[[i]], display = "chao")[[1]][,1], summary(col.est.
ME.core[[i]], display = "chao")[[1]][,2], col = "grey40", lty =
2)
for (i in 1:length(gcp.cores.ME)) lines(summary(gcp.est.
ME.core[[i]], display = "chao")[[1]][,1], summary(gcp.est.
ME.core[[i]], display = "chao")[[1]][,2])

title(xlab = "Number of samples", ylab = "Chao2 estimated
species richness", outer = T, line = 1)

```

```

##NMDS
gcp.nmds <- metaMDS(gcp[,specnumber(gcp, MARGIN = 2) > 1],
trymax = 50)

##Figure 7.6
##Plot with formation names and convex hulls
plot(gcp.nmds, display=c("sites"), choices = c(1,2), type="n",
shrink=FALSE, xlab = "NMDS axis 1", ylab = "NMDS axis 2")
points(gcp.nmds, display=c("sites"), choices = c(1,2),
type="p", col = "grey40", shrink=FALSE)
ordihull(gcp.nmds, gcp.info$Formation, display = "sites", draw
= c("polygon"), label = TRUE)

##TURNOVER
##Enter data - GCP, binned into formations with formation
uniques removed
GCP.fmns <- read.table (file = "Dataset_fmns.txt", header=TRUE,
row.names=1)
fmns.details <- read.table (file = "Formations_details.txt",
header=TRUE, row.names=1)

##Set up list of rarefied matrices and remove unique/zero entry
taxa
GCP.fmns.subs <- vector("list", 1000)
for (i in 1:1000) GCP.fmns.subs[[i]] <- rrarefy(GCP.fmns, 290)
GCP.fmns.subs.nouniques <- lapply(GCP.fmns.subs, function(x)
x[,colSums(x > 0) > 1])

##Set up list of range-through matrices, and combine rowSums
into one 8 x 1000 cell matrix
rangethrough <- vector("list", 1000)

for (i in 1:1000) rangethrough[[i]] <- matrix(0,nrow =
nrow(GCP.fmns.subs.nouniques[[i]]), ncol = ncol(GCP.fmns.
subs.nouniques[[i]]), dimnames = list(rownames(GCP.fmns.subs.
nouniques[[i]]), colnames(GCP.fmns.subs.nouniques[[i]])))

for (i in 1:length(rangethrough)) {
  for (j in 1:ncol(rangethrough[[i]])) rangethrough[[i]]
[min(which(GCP.fmns.subs.nouniques [[i]] [,j] != 0)):max(which
(GCP.fmns.subs.nouniques [[i]] [,j] !=0)), j] <- 1
}

standing.richness <- matrix(0,nrow = 8, ncol = 1000, dimnames =
list(rownames(GCP.fmns), NULL))
for (i in 1:1000) standing.richness [,i] <-
rowSums(rangethrough[[i]])

```

```

##Set-up list of taxon FADs and LADs
taxon.ranges <- vector("list", 1000)
turnover <- function(x) fmns.details[range(which(x != 0)),2]
for (i in 1:1000) taxon.ranges [[i]] <- t(apply(GCP.fmns.subs.
nounsiques [[i]], 2, turnover))

##Convert FAD/LAD matrices to tables, and combine into 8 x1000
cell matrices
last.app.freq <- lapply(taxon.ranges, function (x) as.data.
frame(table(x[,1]), stringsAsFactors = FALSE))
last.appearances <- as.matrix(fmns.details[,2])
colnames(last.appearances) <- "mid.point"
for (i in 1:1000) last.appearances <- merge(last.appearances,
last.app.freq [[i]], by.x = "mid.point", by.y = "Var1", all=T)
last.appearances[is.na(last.appearances)] <- 0
last.appearances <- last.appearances[rev(order(last.
appearances$mid.point)),]
last.appearances <- last.appearances[,2:1001]
last.appearances.prop <- last.appearances/standing.richness

first.app.freq <- lapply(taxon.ranges, function (x) as.data.
frame(table(x[,2]), stringsAsFactors = FALSE))
first.appearances <- as.matrix(fmns.details[,2])
colnames(first.appearances) <- "mid.point"
for (i in 1:1000) first.appearances <- merge(first.appearances,
first.app.freq [[i]], by.x = "mid.point", by.y = "Var1", all=T)
first.appearances[is.na(first.appearances)] <- 0
first.appearances <- first.appearances[rev(order(first.
appearances$mid.point)),]
first.appearances <- first.appearances[,2:1001]
first.appearances.prop <- first.appearances/standing.richness

##Bring together results into summary table, and export
turnover.fmns.results <- matrix(0,nrow = 8, ncol = 15, dimnames
= list(rownames(GCP.fmns), c("Mean.standing.richness",
"M.s.r.+95%", "M.s.r.-95%", "Mean.no.LAD", "M.n.LAD+95%",
"M.n.LAD-95%", "Mean.no.FAD", "M.n.FAD+95%", "M.n.FAD-95%",
"Mean.prop.LAD", "M.p.LAD+95%", "M.p.LAD-95%", "Mean.prop.FAD",
"M.p.FAD+95%", "M.p.FAD-95%")))
quartiles.975 <- function(m) sort(m)[975]
quartiles.25 <- function(m) sort(m)[25]
turnover.fmns.results[,1] <- rowMeans(standing.richness)
turnover.fmns.results[,2] <- apply(standing.richness, 1,
quartiles.975)
turnover.fmns.results[,3] <- apply(standing.richness, 1,
quartiles.25)
turnover.fmns.results[,4] <- rowMeans(last.appearances)

```

```

turnover.fmns.results[,5] <- apply(last.appearances, 1,
quartiles.975)
turnover.fmns.results[,6] <- apply(last.appearances, 1,
quartiles.25)
turnover.fmns.results[,7] <- rowMeans(first.appearances)
turnover.fmns.results[,8] <- apply(first.appearances, 1,
quartiles.975)
turnover.fmns.results[,9] <- apply(first.appearances, 1,
quartiles.25)
turnover.fmns.results[,10] <- rowMeans(last.appearances.prop)
turnover.fmns.results[,11] <- apply(last.appearances.prop, 1,
quartiles.975)
turnover.fmns.results[,12] <- apply(last.appearances.prop, 1,
quartiles.25)
turnover.fmns.results[,13] <- rowMeans(first.appearances.prop)
turnover.fmns.results[,14] <- apply(first.appearances.prop, 1,
quartiles.975)
turnover.fmns.results[,15] <- apply(first.appearances.prop, 1,
quartiles.25)
write.table(turnover.fmns.results, "Turnover_sub_fmns_results.
txt", sep = "\t", row.names = T, col.names = T)

##Setting up matrix of expected first and last appearances under
constant turnover
turnover.fmns.expected <- matrix(0,nrow = 8, ncol = 4, dimnames
= list(rownames(turnover.fmns.results), c("Expected.last", "sd.
last", "Expected.first", "sd.first")))
(expected.last <- sum(turnover.fmns.results[2:7,4])/
sum(turnover.fmns.results[2:7, 1]))
(expected.first <- sum(turnover.fmns.results[2:7,7])/
sum(turnover.fmns.results[2:7, 1]))
turnover.fmns.expected[,1] <- rep(expected.last, nrow(turnover.
fmns.expected))
turnover.fmns.expected[,3] <- rep(expected.first, nrow(turnover.
fmns.expected))
turnover.fmns.expected[,2] <- sqrt((turnover.fmns.
expected[,1]*(1-turnover.fmns.expected[,1]))/turnover.fmns.
results[,1])
turnover.fmns.expected[,4] <- sqrt((turnover.fmns.
expected[,3]*(1-turnover.fmns.expected[,3]))/turnover.fmns.
results[,1])
write.table(turnover.fmns.expected, "Turnover_sub_fmns_
expected.txt", sep = "\t", row.names = T, col.names = T)

```

##Figure 7.7

```

plot(turnover.fmns.results[2:7,13], fmns.details[2:7,1], type
= "n", main = "First appearances", xlab = "Proportional first

```

```

appearances (prop)", ylab = "", bty= "n")
lines(turnover.fmns.expected[2:7,3], fmns.details[2:7,2], col =
"red")
lines(turnover.fmns.expected[2:7,3]+(turnover.fmns.
expected[2:7,4]*1.96), fmns.details[2:7,2], col = "red", lty =
2)
lines(turnover.fmns.expected[2:7,3]-(turnover.fmns.
expected[2:7,4]*1.96), fmns.details[2:7,2], col = "red", lty =
2)
lines(turnover.fmns.results[2:7,13], fmns.details[2:7,2], col =
"blue")

plot(turnover.fmns.results[2:7,10], fmns.details[2:7,1], type
= "n", main = "Last appearances", xlab = "Proportional last
appearances", ylab = "", bty= "n")
lines(turnover.fmns.expected[2:7,1], fmns.details[2:7,2], col =
"red")
lines(turnover.fmns.expected[2:7,1]+(turnover.fmns.
expected[2:7,2]*1.96), fmns.details[2:7,2], col = "red", lty =
2)
lines(turnover.fmns.expected[2:7,1]-(turnover.fmns.
expected[2:7,2]*1.96), fmns.details[2:7,2], col = "red", lty =
2)
lines(turnover.fmns.results[2:7,10], fmns.details[2:7,2], col =
"blue")

##SPECIATION VERSIS IMMIGRATION
##Enter data - first appearance codes for each taxon
first.app <- read.table (file = "First_appearances.txt",
header=TRUE, row.names=1)
immigrants.all <- table(first.app[,1])
immigrants.all <- immigrants.all[c(3, 1, 4, 5, 6, 2, 7, 9)]

##Without sample uniques
gcp.vetted <- gcp[,specnumber(gcp, MARGIN = 2) > 1]
gcp.nosamplesuniques <- cbind(1:150, colnames(gcp.vetted))
first.app <- cbind(first.app, rownames(first.app))
colnames(first.app) <- c("code", "taxon")
colnames(gcp.nosamplesuniques) <- c("ID", "taxon")
gcp.nosamplesuniques <- merge(gcp.nosamplesuniques, first.app)
immigrants.nosampleuniques <- table(gcp.nosamplesuniques[,3])
immigrants.nosampleuniques <- immigrants.nosampleuniques[c(3,
1, 4, 5, 6, 2, 7, 9)]

##Without formation uniques
gcp.fmns.vetted <- GCP.fmns[,specnumber(GCP.fmns, MARGIN = 2)
> 1]

```

```

gcp.nofmnuniques <- cbind(1:126, colnames(gcp.fmnns.vetted))
colnames(gcp.nofmnuniques) <- c("ID", "taxon")
gcp.nofmnuniques <- merge(gcp.nofmnuniques, first.app)
immigrants.nofmnuniques <- table(gcp.nofmnuniques[,3])
immigrants.nofmnuniques <- immigrants.nofmnuniques[c(3, 1, 4,
5, 6, 2, 7, 9)]

##Figure 7.8
par(mfrow = c(3,1))
pie(immigrants.all, main = "A) All taxa (n = 189)", init.angle
= 90, radius = 1)
pie(immigrants.nosampleuniques, main = "B) No sample uniques (n
= 146)", init.angle = 90, radius = 1)
pie(immigrants.nofmnuniques, main = "C) NO formation uniques (n
= 126)", init.angle = 90, radius = 1)

##Tabulate by formation and produce bar chart
fmns.details <- cbind(rownames(GCP.fmnns), 1:8)
turnover <- function(x) fmns.details[range(which(x != 0)),1]
taxon.ranges <- t(apply(GCP.fmnns, 2, turnover))
write.table(taxon.ranges, "Taxon_ranges.txt", sep = "\t", row.
names = T, col.names = T) ##range data for all taxa

##First appearances with formation uniques removed, and bar
plot
taxon.ranges.nouniques <- t(apply(gcp.fmnns.vetted, 2,
turnover))
taxon.ranges.nouniques <- cbind(taxon.ranges.nouniques,
rownames(taxon.ranges.nouniques))
fa <- taxon.ranges.nouniques[,2:3]
colnames(fa) <- c("datum", "taxon")
fa <- merge(fa, first.app)
immigrants.fmn <- table(fa[,2], fa[,3])
immigrants.fmn <- immigrants.fmn[c(4, 2, 3, 6, 1, 5),c(3, 1, 4,
5, 6, 2, 7, 9)]

##Figure 7.9
barplot(t(immigrants.fmn), col=rainbow(9), ylim = c(0, 60),
legend.text = TRUE)

```


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